National Library
of Canada

Canadian Theses Service

Ottawa, Canada
K1A 0N4

Bibliothèque nationale
du Canada

Services des thèses canadiennes

CANADIAN THESES

THÈSES CANADIENNES

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30. Please read the authorization forms which accompany this thesis.

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30. Veuillez prendre connaissance des formules d'autorisation qui accompagnent cette thèse.

THIS DISSERTATION
HAS BEEN MICROFILMED
EXACTLY AS RECEIVED

LA THÈSE A ÉTÉ
MICROFILMÉE TELLE QUE
NOUS L'AVONS REÇUE

NL 339 (r. 86/01)

Canada

0-315-22927-6

National Library of Canada
Canadian Theses Division
Ottawa, Canada
K1A 0N4

Bibliothèque nationale du Canada
Division des thèses canadiennes

6

PERMISSION TO MICROFILM — AUTORISATION DE MICROFILMER

- Please print or type — Écrire en lettres moulées ou dactylographier

Full Name of Author — Nom complet de l'auteur
TERRANCE MICHAEL STOCK

Date of Birth — Date de naissance
11 AUG 1951

Country of Birth — Lieu de naissance
CANADA

Permanent Address — Résidence fixe
DEPT. OF ZOOLOGY
UNIV. OF ALBERTA
EDMONTON, ALBERTA T6G 2E9

Title of Thesis — Titre de la thèse
PATTERNS OF COMMUNITY ECOLOGY AND COEVOLUTION OF INTESTINAL HELMINTHS IN GREBES

University — Université
UNIV OF ALBERTA

Degree for which thesis was presented — Grade pour lequel cette thèse fut présentée
Ph. D.

Year this degree conferred — Année d'obtention de ce grade
1985

Name of Supervisor — Nom du directeur de thèse
DR. JOHN C. HOLMES

Permission is hereby granted to the NATIONAL LIBRARY OF CANADA to microfilm this thesis and to lend or sell copies of the film.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

L'autorisation est, par la présente, accordée à la BIBLIOTHÈQUE NATIONALE DU CANADA de microfilmer cette thèse et de prêter ou de vendre des exemplaires du film.

L'auteur se réserve les autres droits de publication; ni la thèse ni de longs extraits de celle-ci ne doivent être imprimés ou autrement reproduits sans l'autorisation écrite de l'auteur.

Date
AUGUST 2, 1985

Signature
Terrance M. Stock

NL-91 (4/77)

THE UNIVERSITY OF ALBERTA

Patterns of Community Ecology and Coevolution of Intestinal Helminths in Grebes

by

Terrance Michael Stock

©

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF Doctor of Philosophy

Department of Zoology

EDMONTON, ALBERTA

Fall 1985

THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR Terrance Michael Stock

TITLE OF THESIS Patterns of Community Ecology and Coevolution of Intestinal Helminths in Grebes

DEGREE FOR WHICH THESIS WAS PRESENTED Doctor of Philosophy

YEAR THIS DEGREE GRANTED Fall 1985

Permission is hereby granted to THE UNIVERSITY OF ALBERTA LIBRARY to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

(SIGNED) Terrance Michael Stock

PERMANENT ADDRESS:

Department of Zoology
University of Alberta
Edmonton Alberta

DATED July 5 1985

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Patterns of Community Ecology and Coevolution of Intestinal Helminths in Grebes submitted by Terrance Michael Stock in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

....
Supervisor

W. M. Samuel

....

John R. Spence

....

....
External Examiner

Date August 2, 1985

Abstract

The structure and organization of communities of intestinal helminths in a small group of related hosts, grebes (Podicipedidae), were analyzed in order to evaluate the relevance of several alternative hypotheses, including specialization, interaction and coevolution. Communities in four species from Alberta, including 20 *Aechmophorus occidentalis*, 33 *Podiceps grisegena*, 31 *Podiceps nigricollis*, and 7 *Podiceps auritus*, were examined.

Multivariate analysis indicated that three of four hosts had distinctive parasite communities, each characterized by a group of regularly co-occurring and abundant (core) species. Most of these species were specialist parasites in grebes which maintained the bulk of their populations within a single host species (the main host), but frequently were also found in other grebe species, particularly those with similar food habits (the large *A. occidentalis* and *P. grisegena* versus the smaller *P. nigricollis* and *P. auritus*). Distributional patterns of parasites among host species revealed that *A. occidentalis*, *P. grisegena*, and *P. nigricollis* had helminth assemblages that met the prerequisites necessary for communities in which interactions (such as competition) between parasites could be important.

In order to evaluate the evidence for interactive versus isolationist communities, the microhabitat distributions of core species were analyzed. Based on their linear arrangements in the intestines, most helminths demonstrated wide total occupied ranges, but significantly reduced average ranges. Core helminths did not appear to be restricted by their degree of specialization. Overlap between helminths seldom increased when joint population size increased, and the distributions of some species in grebes were affected by others. Interactions contributed to the maintenance of community structure. Nevertheless, distributions of guild members indicated that the communities were not saturated but contained empty niches. In addition, helminths were not evenly spread in niche space. Both are features of isolationist communities. A model of differential selection pressures in different parts of the intestine, based on the theory of habitat selection, was proposed. The model encompasses both isolationist and interactive characteristics. Relatively specialized, r-selected species of absorbers were predicted to predominate in the proximal intestine, K-selected competitionists in the favorable mid-intestine, and opportunistic generalists (and some specialists) in the posterior intestine.

To evaluate coevolutionary constraints on the system, the evidence for co-ordinated genealogies between an important group of core species, the amabiliids, and grebes were examined. A comparison of parasite cladograms with a host phylogenetic scheme disclosed that both co-speciation and zoogeographic events were important. The intestinal helminth communities in grebes appear to represent long-standing associations of coevolved parasites.

Acknowledgements

Conducting this research project and writing this thesis were true learning experiences. I want to acknowledge many teachers I had along the way. First, I want to express my sincerest thanks to my supervisor, John Holmes. Dr. Holmes guided, encouraged, and when necessary pushed me. Not only was John Holmes always interested in the progress of the research, but he was also always concerned for the welfare of his students. This personal interest, combined with his first-hand knowledge of all aspects of this study, made it easy to not get discouraged, even while sitting in a pile of slushy hail, in a canoe on Cow Lake during a thunderstorm.

Throughout the course of my studies, I was blessed to be surrounded by a group of graduate students, visiting professors, post-doctoral fellows and technicians who freely shared both their friendship, and their stimulating and intelligent arguments. In particular, I take great pleasure in acknowledging Al Bush, Eric Butterworth, John Aho, and Jim Munger. Each offered a different perspective. Al taught me to think about the underlying significance of facts and about generalizing. He did this by example with his own, excellent scientific work. Eric taught me that science involves sacrifice, persistence, and dedication. John showed me that science should be fun. He was an excellent field companion and I thank him for preventing me from axing and burning a Zodiac inflatable boat. Jim made me appreciate the philosophical aspects of science; his support and encouragement went far in helping me to realize that there might be some value to what I was doing. Many ideas presented in this dissertation are the results of an evolutionary process, starting from informal discussions and arguments among Al, Eric, John, Jim, John Holmes, and myself.

I want to acknowledge members of my advisory committee, Dr. D.A. Boag, Dr. Wm. Samuel, and Dr. J.R. Spence, for critically reviewing my work, for offering valuable suggestions, and for making editorial comments on earlier drafts of chapters of this thesis. Dr. C.R. Kennedy presented many interesting comments and questions during my thesis defence. I thank Dr. R.W. Storer for sharing his ideas on the evolutionary history of grebes.

I received excellent technical assistance throughout all phases of this study. Al Bush, Eric Butterworth, John Aho, John Holmes, Dennis Pfeffer, Mark Steinhilber, Al Shostak, Rob Kralka and Karen Nielsen helped me collect grebes. Ron Seward and Randy Mandryk prepared histological sections. Dr. John Addicott and Mr. Norris Weimer helped greatly with computer analysis of data (both showed tremendous patience!).

I owe a special debt of gratitude to Dr. Holmes, Dr. Samuel, and Dr. J. Mahrt who allowed me to defer most of the duties of my job as parasitology laboratory technologist in order to complete this thesis. J. Brent Gray, Leslie Robb and Simone Helluy took on many of my responsibilities during this time.

Research was supported financially by a Natural Sciences and Engineering Research Council of Canada grant to Dr. Holmes, and by a Boreal Institute grant to me. In addition, I thank the Department of Zoology, particularly Drs. Chia, Boag, Peter and Spencer, for support with graduate teaching assistantships, funds to attend scientific conferences, and when necessary, time extensions.

On a personal note, I thank Jim Selby, Judy Samoil, and the Samoil family for giving me a warm and friendly home in Edmonton, and for helping me find my contact lenses. I thank Judith Samson for her friendship and for her encouragement. I extend a final, very personal thank you to Debbie Thomson. Debbie always found time to encourage and support me in the completion of this work, even while she was enduring her own problems. Her courage and spirit during this time will always be remembered.

Table of Contents

Chapter Page

I. General Introduction 1

- A. Literature Cited 14

II. Patterns of Distribution of Intestinal Helminths in Grebes: Prerequisites for Interactive Communities 17

- A. Abstract 17
- B. Introduction 18
- C. Materials and Methods 21
- D. Results 26
- E. Discussion 58
- F. Literature Cited 69

III. Functional Relationships and Microhabitat Distributions of Intestinal Helminths in Grebes: The Evidence for Interactive Communities 72

- A. Abstract 72
- B. Introduction 73
- C. Materials and Methods 76
- D. Results 79
- E. Discussion 140
- F. Literature Cited 160

IV. General Discussion: Coevolutionary Constraints on Community Structure 164

- A. Introduction 164
- B. Host Phylogeny 170
- C. Zoogeography of Grebes 180
- D. Phylogeny of the Amabiliidae 185
- E. Comparison of Host and Parasite Genealogies ... 196

F. Implications for Intestinal Helminth Community Structure 205

G. Bibliography 209

List of Tables

Chapter 2.

Table Page

1. Lakes in Alberta where grebes were collected 24
2. Prevalences and intensities of intestinal helminths in grebes..27
3. General characteristics of helminth communities 30
4. Associations of helminths in grebes...................35
5. First three principal components of abundances of parasites in grebes.................................55
6. Core, secondary and satellite species in grebes and waterfowl...64

Chapter 3.

Table Page

1. Morphological characteristics of grebes...............80
2. Distribution of helminths in grebes...................82
3. Locations of helminths in *Aechmophorus occidentalis*....91
4. Locations of helminths in *Podiceps grisegena* 92
5. Locations of helminths in *Podiceps nigricollis*.........93
6. Locations of helminths in *Podiceps auritus* 94
7. Spearman rank correlations of locations of helminths in grebes...102
8. Effects of population size on distributions of helminths in *A. occidentalis*.......................104

9. Effects of population size on distributions of helminths in *P. grisegena*......105
10. Effects of population size on distributions of helminths in *P. nigricollis*......106
11. Effects of population size on distributions of helminths in *P. auritus*......107
12. ANOVA of distributions of helminths in four species of grebes......113

Chapter 4

Table Page
1. Distribution of grebes of the world......171
2. Character states of amabiliids......187
3. Characters of 18 species of amabiliids......188
4. Hosts of amabiliid tapeworms......197

List of Figures

Chapter 1.

Figure Page

1. Distributions of four species of grebes in Alberta.....8
2. Seasonal biology of *Aechmophorus occidentalis*..........10

Chapter 2.

Figure Page

1. Lakes in Alberta where grebes were collected...........23
2. Frequency distributions of parasite prevalences 33
3. Cumulative number of helminth species..................37
4. Recurrent groups in four species of grebes.............41
5. Recurrent groups in 91 grebes..........................43
6. Cluster dendrogram of helminths in grebes..............47
7. Cluster dendrogram of grebes based on presence/absence of intestinal parasites..............50
8. Cluster dendrogram of grebes based on abundances of intestinal parasites..................................53
9. Distribution of grebes in principal components space...57
10. Patterns of exchange of intestinal helminths among four species of grebes................................61
11. Arrangements of grebes along three measures of helminth community structure.........................68

Chapter 3.

Figure Page

1. Relationships of morphological features to 20 intestinal sections....78
2. Distribution of vacant sections....85
3. Mean number of helminth species per intestinal section.87
4. Mean number of helminths per intestinal section....89
5. Frequency distribution of locations of mean medians of helminths....96
6. Distributions of core, secondary and recurrent group species....99
7. Distribution of Spearman rank correlation rho values..101
8. Total occupied ranges of intestinal helminths 109
9. Standard deviations of mean median values....112
10. Comparison of locations of species common to four species of grebes....115
11. *Dioecocestus asper* in the intestine of *Podiceps grisegena*....119
12. Mean number of villi per intestinal section in grebes with, and without *D. asper*....121
13. Mucosal widths per intestinal section in grebes with, and without *D. asper*....123
14. Distributions of core helminths in *P. grisegena* with, and without *D. asper* 126
15. Differences in mean number of species and mean number of individuals in intestines with, and without *D. asper*....129
16. Distributions of congeneric helminths in grebes......132

17. Reductions of overlaps of realized niches of core helminths....................................137
18. Significant increases in overlap with increasing joint population size.............................139
19. Distribution of three guild members in the intestines of grebes.................................144
20. A model of differential selection pressures acting on absorber parasites..............................149
21. Correlation between hook length and position of cestodes in grebes.................................152

Chapter 4.

Figure Page
1. Phylogenetic scheme of the Podicipedidae..............173
2. A zoogeographic model of distribution of grebes.......183
3. A cladogram of the genus *Schistotaenia* 191
4. A cladogram of the genus *Tatria*.......................195
5. A comparison of *Schistotaenia* and grebe genealogies...199
6. A comparison of *Tatria* and grebe genealogies..........203

I. General Introduction

A primary objective in the study of a community of organisms is to determine if consistent and predictable patterns of species abundances and methods of resource exploitation occur; in short, if the community is structured. Alternatively, the community may represent a random assemblage of species that are relatively insensitive to the presence of other species, a disorganized and unpredictable community. Price (1984) presented several alternative paradigms to explain the degree of organization noted in a community; however, he recommended that a community oriented study should not seek to determine which of the alternatives is relevant, but should ask which paradigm is most important for a defined set of resources. Similarly, Holmes and Price (1985) examined several alternative hypotheses that endeavored to judge if, and how communities of parasites are organized. Again, they pointed out that the alternatives are not mutually exclusive, so that the challenge was not to reject one or more of the hypotheses, but to evaluate the relative importance of each in a given community, and eventually to evaluate the conditions under which each process becomes predominant.

Hair (1975) and Bush (1980) investigated the structure of intestinal helminth communities in lesser scaup, *Aythya affinis*. They detected repetitive associations of some parasites and predictable microhabitat distributions of helminths within each bird and concluded that interspecific interactions among helminths were important as an organizing force. Butterworth (1982) studied the structure and organization of intestinal helminth communities in several species of waterfowl and found a gradation of communities ranging from those that were large, complex and predictable, to those that were small, simple and highly variable.

Butterworth (1982) and Bush and Holmes (MSa) showed that the helminth communities of waterfowl that were large and complex contained two major elements: a group of common and regularly co-occurring species and a larger, indeterminant element. Hanski (1982) postulated that many communities were structured in this way. Hanski defined species that were locally abundant and that regularly co-existed as "core" species, while the unpredictable segment of the community was composed of "satellite" species.

The dichotomy between these two elements in a community is important. Not only were core species predicted to be ecologically adjusted and evenly spread in niche space (Hanski, 1982), but Holmes and Price (1985) observed that the potential for coevolutionary forces to act would be much greater within the core species element. Butterworth (1982) suggested that core species in the complex communities that he studied were "coadapted", but a coevolutionary analysis of his system was not possible because he did not have the opportunity to examine representatives of all of the numerous, sympatric host species that were present.

Conversely, Hair (1975) and Bush (1980) could not assess coevolutionary constraints in their system because they dealt with a single host species. Therefore, analysis of the structure and organization of communities of helminths in a small group of related hosts, in order to evaluate the importance of alternative hypotheses including coevolution, is desirable.

Price (1984) advocated two different approaches to selecting communities for such an analysis. One approach involved selecting a community of organisms, "almost at random", so that no preconceived bias for one of the alternative paradigms would affect the objective testing among hypotheses. The second approach involved selection of coexisting, phylogenetically related species, thus permitting a particularly potent examination of one of the hypotheses, competition between species.

This study is a combination of the two approaches. The chosen hosts, grebes (Podicipediformes), are closely related members of a phylogenetically old group, highly specialized for foot-propelled diving (Storer, 1963). Four species coexist for much of the year on freshwater lakes in Alberta (Salt and Salt, 1976). These species differ greatly in size and food habits (Palmer, 1962; Cramp and Simmons, 1977), potentially exposing them to an "almost random" assortment of parasitic helminths. The following two sections will discuss the applicability of intestinal helminths and grebes for examining predictions arising from some of the alternative hypotheses concerning the organization of parasite communities.

Applicability of Using Intestinal Parasites

Dayton and Tegner (1984) stated that, "The proper integration of spatial and temporal scales is perhaps the most important challenge in ecology today". Intestinal helminth assemblages provide suitable subjects for an examination of such scales in a community ecology study because of the obvious levels of organization that are represented. The first level of study is the infracommunity (those parasites infecting an individual host, Bush 1980). The boundaries of infracommunities are discrete and non-ambiguous. Direct interactions between the host and its parasites, as well as among the parasites themselves, occur at this level. Because each individual host represents a separate infracommunity, repeated samples of hosts allow for a statistical investigation of community structure and similarity (Bush, 1980).

Intestinal parasites represent a subset of the infracommunity. Intestines are the most favored site for helminth parasites (Mettrick and Podesta, 1974); therefore, communities are often species rich with abundant populations. Because the intestine is a continuous, essentially linear gradient with distinct endpoints (the pylorus and the ileo-caecal junction), and most of the morphological and physiological characteristics are strongly correlated with location, the use of resources can be assessed (in large part) by location (Bush and Holmes, MSb).

The study of intestinal helminth communities suffers from two disadvantages. First, in order to determine accurately the kinds and numbers of parasites present, the infracommunity has to be destructively examined, precluding either repeated observations or manipulations of the same infracommunity. Second, experimental infections, which are alternatives to perturbing existing systems, can be difficult. The complex life cycles of most helminths, combined with the difficulties of artificially feeding and rearing hosts, often prohibit experimentation.

The second level of study is the host species; here, the helminths form what Root (1967) called a component community. Again, the boundaries are discrete and non-ambiguous. The frequency of interactions between parasites is determined at this level; repeated and predictable units within the community (core species), which have the potential to interact frequently, can be identified. As at the first level, communities can be described statistically. Associations of parasites in birds of different sex and age, and in birds from different habitat zones, lakes, years or seasons, represent subsets of the community at the level of host species.

The third level of study is the host community, the helminths of which form a compound community. Since local host populations and distributions fluctuate, the boundaries at this level are less distinct. Mechanisms such as host specificity, exchange of parasites among hosts, and coevolution apply at this level. The influence of phylogeny can be assessed to extend the scale from patterns seen in the present to those of the inferred evolutionary past.

Applicability of Using Grebes

Grebes are particularly appropriate hosts to use in a parasite community ecology study. In Alberta, three species, *Aechmophorus occidentalis* (western grebe), *Podiceps grisegena* (red-necked grebe) and *Podiceps nigricollis* (eared grebe) are widely distributed and common in large numbers on lakes (Fig. 1). A fourth species, *Podiceps auritus* (horned grebe), usually nests on smaller bodies of water but during the later part of the summer may be found on lakes (Salt and Salt, 1976). A fifth species that is widespread in Alberta, *Podilymbus podiceps* (pied-billed grebe), is very rare on lakes, preferring to nest solitarily on woodland ponds and prairie sloughs (Salt and Salt, 1976). None were collected for use in this study.

Grebes are seasonal residents in Alberta. The birds migrate to coastal areas and estuaries along the Pacific and Gulf of Mexico during winter, but return to Alberta to spend the long breeding season on freshwater ponds, potholes, sloughs and lakes (Fig. 2). Most freshwater derived parasites are probably lost during the fall migration and residence in marine conditions (as was found for

Figure 1. The distributions of four species of grebes, Podicipedidae, in Alberta, Canada. (Based on information in Salt and Salt, 1976). A = *Aechmophorus occidentalis*, B = *Podiceps grisegena*, C = *Podiceps auritus*, D = *Podiceps nigricollis*.

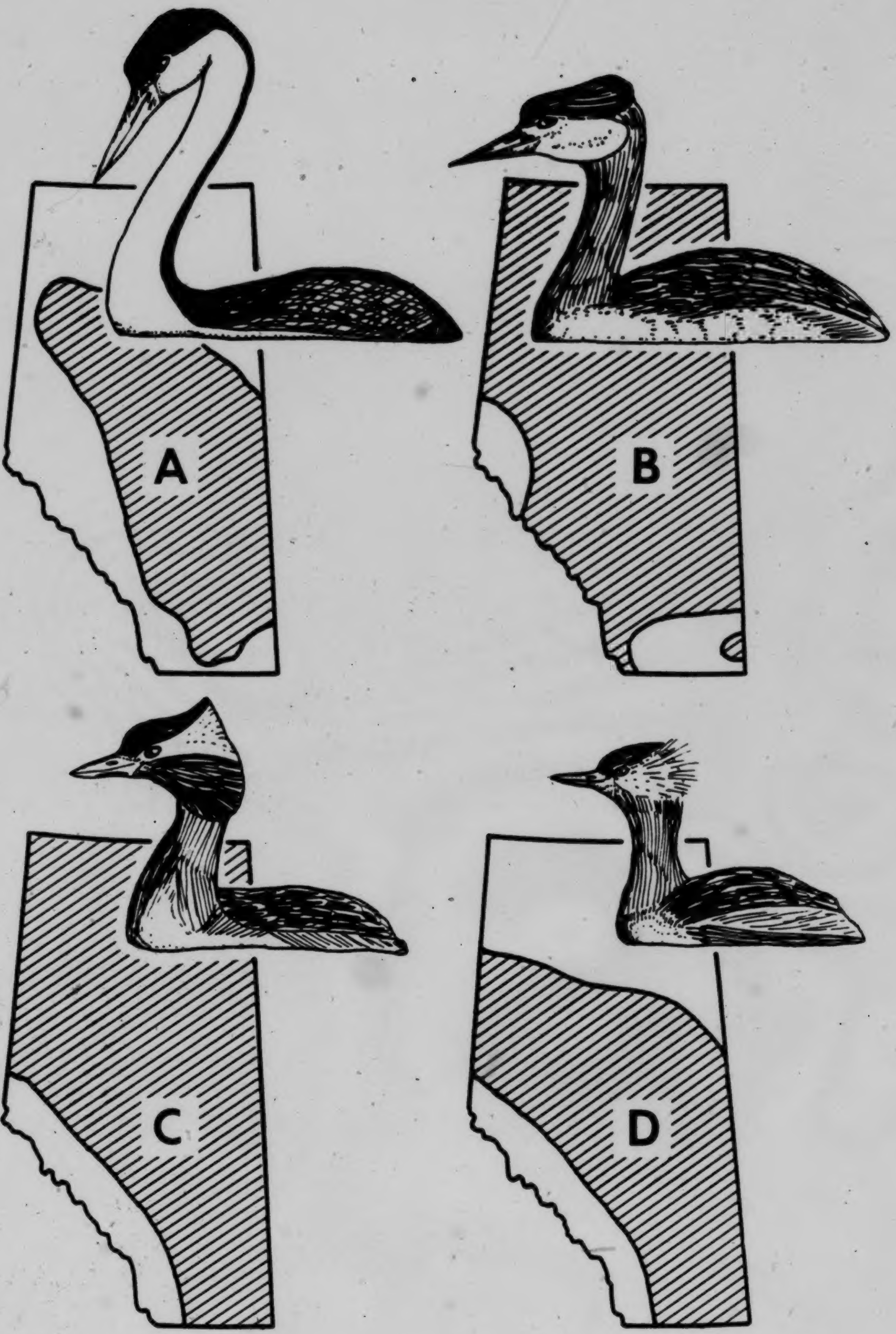
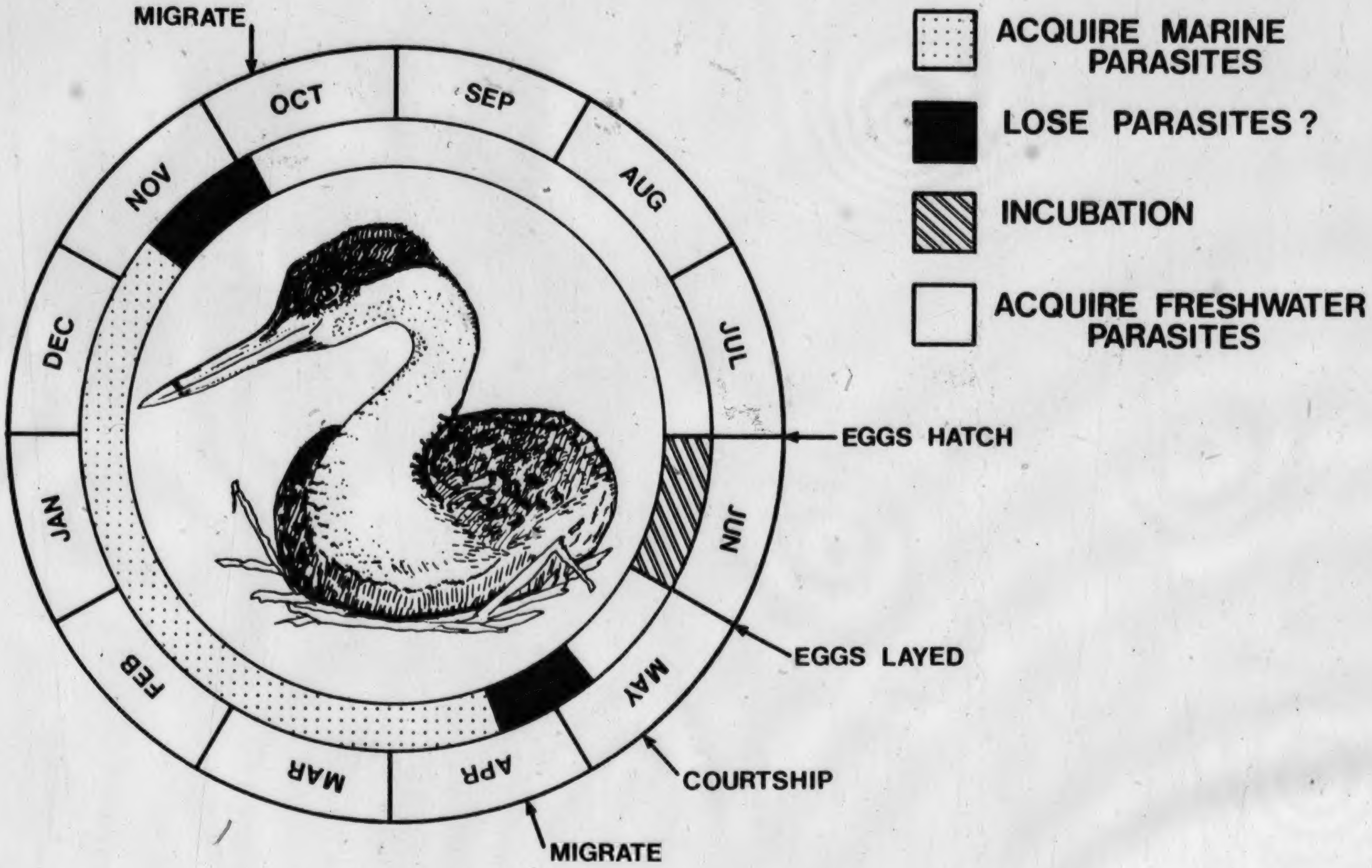

A
B
C
D

Figure 2. The seasonal biology of a grebe in Alberta, using Aechmophorus occidentalis as an example, with the presumed effects on the intestinal parasite fauna.


MIGRATE
OCT
SEP
AUG
JUL
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
EGGS HATCH
EGGS LAYED
COURTSHIP
MIGRATE
ACQUIRE MARINE PARASITES
LOSE PARASITES ?
INCUBATION
ACQUIRE FRESHWATER PARASITES

Arctic-nesting geese by Neraasen, 1970). Freshwater parasites, however, are quickly reacquired during the breeding season (Gallimore, 1964).

Because both male and female birds share in nest duties and rearing young (Kevan, 1970), few sex related differences in parasite burdens were expected or found (Gallimore, 1964). Because feeding by both sexes is reduced during incubation, a minor reduction in parasite populations can occur during this period.

Two of the species, *P. grisegena* and *P. auritus*, are territorial and banding studies have shown site fidelity. For example, mated pairs of *P. auritus* returned to defend the same territory for several years (Ferguson, 1981). Colonial species also appear to consistently use the same lakes. For example, colonies of *P. nigricollis* and *A. occidentalis* have been observed and banded at Beaverhills Lake, Alberta since the 1920's (Lister, 1979). Grebes in general are considered poor flyers. The evidence indicates that grebes are probably faithful to their lake of residence, and exposed to the same local populations of parasites throughout the breeding season.

Taxonomic groundwork on the parasites of grebes, and general information on associations of parasites with host sex, age, food habits and habitat in Alberta were established by Gallimore (1964). Significant differences in parasite burdens were noted in different age groups, and between birds from different habitats (*e.g.*, sloughs *vs.*

ponds). To reduce variability, only adult birds collected on lakes were considered in this study. Food habits are important in determining the composition of the intestinal parasite communities (Gallimore, 1964). Palmer (1962), Borodulina (1976), Cramp and Simmons (1977) and Fjeldsa (1983) indicate that grebes have different, but overlapping diets. *A. occidentalis* eats mostly fish, *P. grisegena* consumes both fish and invertebrates, *P. auritus* eats small fish and invertebrates and the diet of *P. nigricollis* is composed largely of invertebrates, although occasionally small fish are eaten. The overlapping diets suggest that grebes are often exposed to the same parasites; however, the degree of exposure to specific species of parasites probably varies extensively.

Grebes are an ancient group of specialized diving birds with uncertain affinities. Storer (1960), Stegman (1974), Feduccia (1980) and Korzun (1981) suggested that grebes were derived from gruiform ancestors and that similarities with loons (Gaviiformes) and Cretaceous diving birds (*Hesperornis* and *Baptornis*) resulted from convergence. Cracraft (1982), however, presented morphological evidence which indicated that grebes, loons, *Hesperornis* and *Baptornis* were members of a monophyletic group, the Gaviomorphae. In spite of this difference in the interpretation of relationships, it seems indisputable that grebes have existed, essentially unchanged, as a group of specialized divers for a long time. As such, it is reasonable to suppose that grebes are infected with a suite of host specific, characteristic parasites. Extensive behavioral and morphological studies of grebes (Storer, 1963) permits an analysis of the phylogenetic relationships among the grebes, which can be used to assess the evidence for coevolution and colonization by different groups of helminths.

Organization of the Thesis

The second chapter of this thesis will deal with the patterns of parasite distribution among host species. The communities will be described in terms of relative size, complexity and predictability (=similarity). Community structure will be assessed to determine if predictable core units occur, and the contributions of host specificity and host food habits to maintaining patterns of parasite distribution will be evaluated.

The third chapter will deal with the patterns of parasite distributions within individual hosts. The relative roles of microhabitat specialization versus limitation through interactions with other helminth species will be examined. As recommended by Price (1984) and Holmes and Price (1985), the conditions under which each of these mechanisms is acting will be examined.

The final section of this thesis, Chapter 4, will be an attempt to match host and parasite phylogenies in order to identify the presence of heirloom parasites (those that coevolved with their hosts: Sprent, 1969). Patterns of resource use, identified in Chapters 2 and 3, can then be interpreted in the light of evolutionary history. If some parasites have a long association with their host, and frequently co-occur in the present, then the evidence will suggest that conditions have favored a coevolved complex of heirloom parasites. Alternatively, if the host and parasite genealogies do not collate, then the evidence will suggest that communities are formed by parasites that have had little coincident history, and any patterns of complementary resource utilization will suggest colonization by species with preadaptive specializations. Therefore, assessment of the patterns of coevolution will provide a synthesis of ecological information collected at the individual host, host species, and host community levels of organization.

A. Literature Cited

Borodulina, T.L. 1976. Specific food habits and some adaptations of Palearctic grebes. (In Russian.) Mosk. Obsch. Ispyt. Prir. Byull. Otdel. Biol. 81:10-22.

Bush, A.O. 1980. Faunal similarity and infracommunity structure in the helminths of lesser scaup. Ph.D. thesis, Univ. of Alberta, Edmonton. 254 pp.

Bush, A.O., and J.C. Holmes. MSa. Intestinal helminths of lesser scaup ducks: Patterns of association. Submitted to Can. J. Zool. 1985.

Bush, A.O., and J.C. Holmes. MSb. Intestinal helminths of lesser scaup ducks: An interactive community. Submitted to Can. J. Zool. 1985.

Butterworth, E.W. 1982. A study of the structure and organization of intestinal helminth communities in ten species of waterfowl (Anatinae). Ph.D. thesis, Univ. of Alberta, Edmonton. 284 pp.

Cracraft, J. 1982. Phylogenetic relationships and monophyly of loons, grebes, and hesperornithiform birds, with comments on the early history of birds. Syst. Zool. 31:35-56.

Cramp, S., and K.E.L. Simmons. 1977. Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic. Vol. 1. Ostrich to Ducks. Oxford Univ. Press, Oxford. 722 pp.

Dayton, P.K., and M.J. Tegner. 1984. The importance of scale in community ecology: A kelp forest example with terrestrial analogs. pp. 457-481 In P.W. Price, C.N. Slobodchikoff and W.S. Gaud (eds.), A New Ecology. John Wiley & Sons, New York. 515 pp.

Feduccia, A. 1980. The Age of Birds. Harvard Univ. Press, Cambridge, Mass. 196 pp.

Ferguson, R.S. 1981. Territorial attachment and mate fidelity by horned grebes. Wilson Bull. 93:560-561.

Fjeldsa, J. 1983. Ecological character displacement and character release in grebes, Podicipedidae. Ibis 125:463-481.

Gallimore, J.R. 1964. Taxonomy and ecology of helminths of grebes in Alberta. M.Sc. thesis, Univ. of Alberta, Edmonton. 180 pp.

Hair, J.D. 1975. The structure of the intestinal helminth communities of lesser scaup (*Aythya affinis*). Ph.D. thesis, Univ. of Alberta, Edmonton. 92 pp.

Hanski, I. 1982. Dynamics of regional distribution: The core and satellite species hypothesis. Oikos 38:210-221.

Holmes, J.C., and P.W. Price. 1985. Communities of parasites. Chapt. 9 In D.J. Anderson and J. Kikkawa (eds.), Community Ecology: Pattern and Process. Blackwell Sci. Co., Oxford. (in press)

Kevan, C.L. 1970. An ecological study of red-necked grebes on Astotin Lake, Alberta. M.Sc. thesis, Univ. of Alberta, Edmonton. 80 pp.

Korzun, L.P. 1981. On the phylogenetic relationships between divers (Gaviiformes) and grebes (Podicipediformes). (In Russian.) Zool. Zhur. 60:1523-1532.

Lister, R. 1979. The Birds and Birders of Beaverhills Lake. Edmonton Bird Club, Publ., Edmonton, Alberta. 264 pp.

Mettrick, D.F., and R.B. Podesta. 1974. Ecological and physiological aspects of helminth-host interactions in the mammalian gastrointestinal canal. Adv. Parasit. 12:183-278.

Neraasen, T.G. 1970. Ecology of the helminths of three species of arctic-nesting geese with particular reference to the lesser snow goose (*Chen caerulescens caerulescens*): A community analysis. M.Sc. thesis, Univ. of Alberta, Edmonton. 136 pp.

Palmer, R.S. 1962. Handbook of North American Birds. Vol. 1. Loons through Flamingos. Yale Univ. Press, New Haven, Conn. 567 pp.

Price, P.W. 1984. Alternative paradigms in community ecology. pp. 353-383 In P.W. Price, C.N. Slobodchikoff and W.S. Gaud (eds.), A New Ecology. John Wiley & Sons, New York. 515 pp.

Root, R.B. 1967. The niche exploitation pattern of the blue-gray gnat catcher. Ecol. Monog. 37:317-350.

Salt, W.R., and J.R. Salt. 1976. The Birds of Alberta. Hurtig Publ., Edmonton, Alta. 498 pp.

Sprent, J.F.A. 1969. Evolutionary aspects of immunity in zooparasitic infections. pp. 6-32 In G.J. Jackson, R. Herman and I. Singer (eds.), Immunity to Parasitic Animals. Vol. 1. Appleton-Century-Crofts, New York.

Stegman, B.K. 1974. On the phylogenetic relationships between the families Gaviidae and Podicipedidae. (In Russian.) Ornithologia 11:6-19.

Storer, R.W. 1960. Evolution of the diving birds. Proc. XII Intern. Ornithol. Congr. pp. 694-707.

Storer, R.W. 1963. Courtship and mating behavior and the phylogeny of grebes. Proc. XIII Intern. Ornithol. Congr. pp. 562-569.

II. Patterns of Distribution of Intestinal Helminths in Grebes: Prerequisites for Interactive Communities

A. Abstract

The importance of host specificity in determining the structure of intestinal helminth communities can be assessed by studying the pattern of exchange of parasites among taxonomically or ecologically related hosts. Thirty-four species of parasites were recovered from four species of grebes from lakes in Alberta.

The communities were moderately large and complex. Patterns of similarity among the communities, as assessed by cluster and principal components analyses, revealed distinctive infracommunities (parasites within a species of host) in *Aechmophorus occidentalis*, *Podiceps grisegena* and *Podiceps nigricollis*. The community in *Podiceps auritus* overlapped with those of *P. grisegena* and *P. nigricollis*. Frequency distributions of prevalences of parasites for the three hosts with distinctive communities were bimodal, suggesting the presence of "core" (frequent and locally abundant) and "satellite" (infrequent and unpredictable) components. Recurrent group analysis, a method of isolating species that commonly co-occur, confirmed the presence and identity of core species.

Core species were largely grebe specialist parasites. Few were strictly host specific. Most were shared among hosts, with the bulk of the population of each occurring in

one host species. Sharing was particularly significant between the large, fish-eating grebes (*A. occidentalis* and *P. grisegena*) and the smaller, mainly invertebrate-eating grebes (*P. nigricollis* and *P. auritus*). As a result, the identities and relative abundances of core species in each community were highly predictable. Because the organization of grebe helminth communities included significant proportions of commonly co-occurring species, the necessary prerequisites for communities that are structured through interactions between species were met.

B. Introduction

Holmes and Price (1985) suggested that communities of parasites occurred in two distinguishable forms: interactive and isolationist. Interactive communities were most likely in assemblages of species with high probabilities of colonization with relatively large populations, so that the potential for interactions would be great. Interactive communities are likely in component communities (species associated with a distinct microenvironment: Root, 1973) that include many species of helminth parasites that regularly co-occur. Intestinal helminths of lesser scaup, *Aythya affinis*, display such a community (Bush and Holmes, MS).

Isolationist communities would be expected in assemblages of parasites with low or highly variable transmission rates, leading to unsaturated, non-equilibrium communities, which would provide few opportunities for interspecific interactions. In such communities, microhabitat specialization by small, immobile species to exploit a coarse-grained environment would be expected to produce communities of species closely adapted to their host, and to specific sites within that host, but not to other, co-habiting parasites that they infrequently encounter (Price, 1984). Monogenean flukes on the gills of marine fish display such communities (Rohde, 1978).

In order to test the evidence for interactive or isolationist communities, an examination of the communities for the presence of repeated, predictable units is a prerequisite. Hanski (1982) noted that in many systems, the average abundance of a species in a patch of habitat was positively correlated with the proportion of patches in which it was found. As a result, he could distinguish two types of species - "core" species, which were regionally common, locally abundant and therefore, regularly co-occurred, and "satellite" species, which occurred unpredictably and in low numbers.

Although Hanski suggested that an adequate test of the core-satellite species hypothesis was simply to determine if the distribution of species' regional frequencies was bimodal, no specific, objective method to identify species as core or satellite was advocated. However, earlier Fager (1957), Fager and McGowan (1963) and Fager and Longhurst (1968) had suggested an objective analysis, recurrent group analysis, to isolate groups of species that regularly co-occur. In effect, Fager's recurrent group analysis can be used to distinguish Hanski's core species.

Because intestinal parasites, once inside a host, are essentially "fixed" and unable to move to another host, the process of habitat selection by parasites has taken on special significance denoted by the term host specificity. Although a species of parasite may occur in several species of hosts, often one host harbors the bulk of that parasites' breeding population. This host has been termed the "main" or "required" host (Holmes *et al.*, 1977). The role host specificity plays in determining the structure of helminth communities can be assessed by studying the pattern of exchange (or sharing) of parasites among taxonomically or ecologically related host species (Holmes *et al.*, 1977).

One mechanism that contributes to the sharing of parasites among hosts and the concentration of a parasite in a main host is the food habits of those hosts. Obvious selection pressures on parasites to ensure transmission to appropriate hosts have led to many adaptations of parasites to facilitate infection (see review in Holmes, 1976). Predator-prey relations have a significant effect on the composition and structure of helminth communities.

This chapter will describe and examine the communities of intestinal helminths in four species of grebes, western (*Aechmophorus occidentalis*), red-necked (*Podiceps grisegena*), eared (*Podiceps nigricollis*), and horned

(*Podiceps aurutus*). Data presented will show that three of four hosts had distinctive parasite communities, with high proportions of common and abundant core species, so that the prerequisites for interactive communities are met. Both host specificity and the differentiated but overlapping food habits of grebes play significant roles in defining and maintaining intestinal helminth community structure.

C. Materials and Methods

Grebes were collected during the breeding season (May to September) from nine lakes throughout Alberta (Fig. 1). Lakes chosen represented diverse physiographic types from deep, large and oligotrophic (*e.g.*, Bistcho) to shallow, small and eutrophic (*e.g.*, Bellshill) (Table 1); they had large populations of one or more species of grebe and/or grebes had been collected there previously as part of a more inclusive sampling program (see Bush, 1980; Butterworth, 1982).

Birds were shot, immediately weighed, and the intestinal tracts were tied off at the pyloric sphincter and large intestine - cloacal junction, removed to an enamel or plastic pan, and frozen by flooding with 98% ethanol cooled to approximately -70°C with dry ice. This procedure restricted post-mortem migration of helminths and preserved the morphology of fragile cestodes (Hair and Holmes, 1975; Bush and Holmes, MS). Intestines were placed into individually labelled plastic bags and kept frozen until

Figure 1. Nine lakes in Alberta from which grebes were collected.

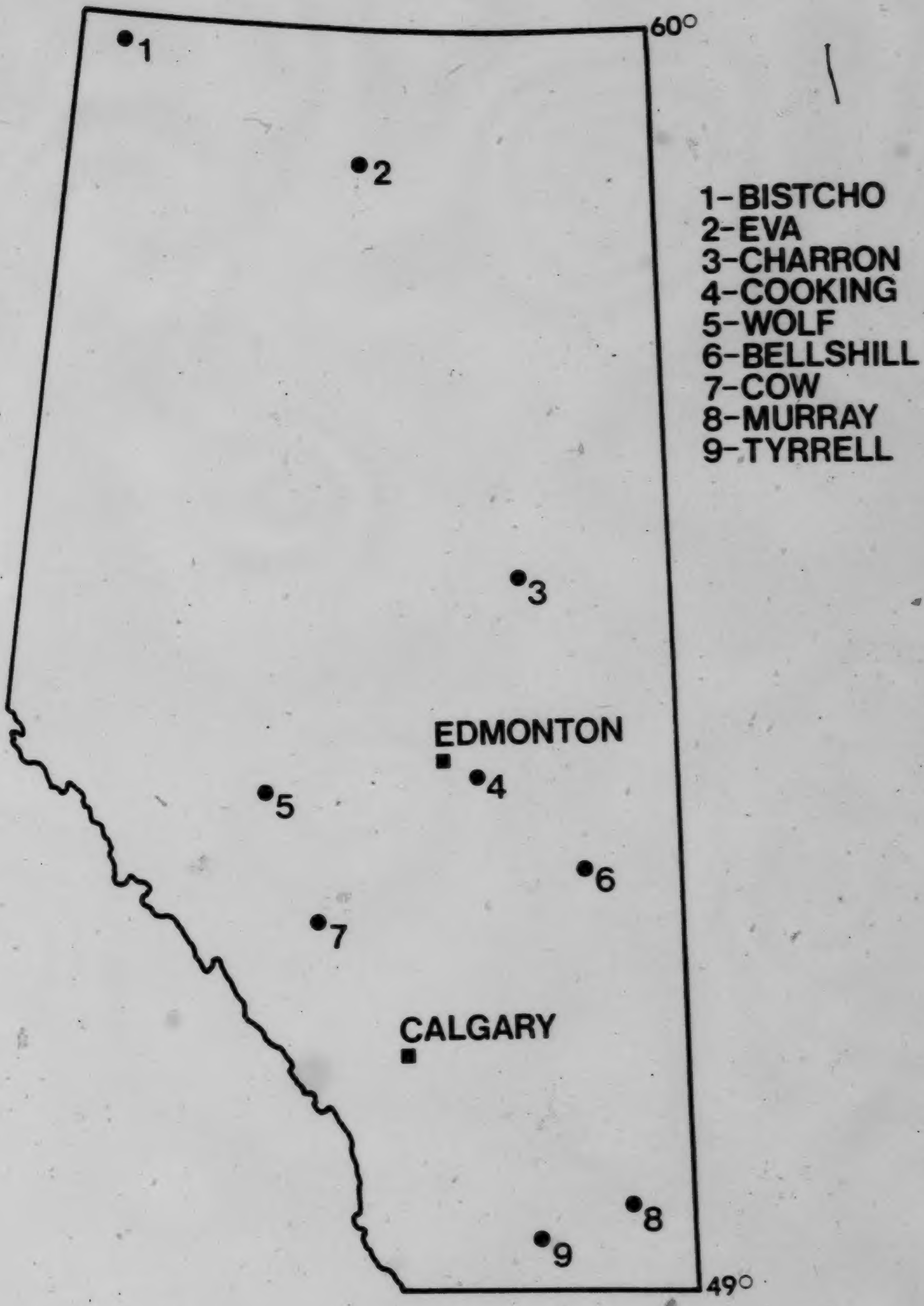

60°
1
2
1-BISTCHO
2-EVA
3-CHARRON
4-COOKING
5-WOLF
6-BELLSHILL
7-COW
8-MURRAY
9-TYRRELL
3
EDMONTON
4
5
6
7
CALGARY
8
9
49°

Table 1. Physical characteristics of nine lakes in Alberta from which grebes were collected. Ao = *Aechmophorus occidentalis*, Pg = *Podiceps grisegena*, Pn = *Podiceps nigricollis*, Pa = *Podiceps auritus*.

Lake	Area (ha)	Shoreline (km)	Mean Depth (m)	No. of Grebes Collected Ao	Pg	Pn	Pa
Bellshill	367	11.2	1.0	1	0	12	3
Bistcho	41396	164.8	3.6	0	4	0	0
Charron	838	35.8	3.6	11	8	4	0
Cooking	3512	57.2	1.5	0	0	4	0
Cow	996	13.3	2.4	8	17	4	4
Eva	1625	22.1	5.2	0	3	0	0
Murray	1730	34.1	1.8	0	0	4	0
Tyrrell	393	14.2	4.0	0	0	3	0
Wolf	233	8.1	4.2	0	1	0	0

examination.

In the laboratory, each intestinal tract was partially thawed and the total length of the small intestine was measured. The small intestine was divided into 20 equal sections, each of which was placed into a vial and refrozen until examined. The large intestine and caeca were also placed in separate vials.

Each intestinal section was examined separately; worms in each section were identified and counted. When more than 500 helminths of a species (generally small cestodes) were encountered in a section (10% of sections), the long, heavy-bodied and rare helminths in the section were removed, identified and counted individually. The remaining helminths and intestinal contents were washed by repeated sedimentation in saline, brought to a volume of 100 ml., and two 10% aliquot samples were removed. Helminths in the subsamples were identified and counted. If the number of common helminths in the two subsamples differed by more than 15%, a third subsample was censused. The sum of the counts in the subsamples was used to estimate the total number of individuals of the common species in that section (Bush and Holmes, MS). Large parasites were blotted dry and weighed to the nearest 0.01 g. Representative specimens were fixed and preserved for preparation of permanent slides. Voucher specimens were deposited in the University of Alberta Parasite Collection (UAPC 11074-11100).

Cluster analyses and distance matrices were determined by the cluster program in MIDAS (Fox and Guire, 1976). Data were log transformed and standardized. Infection parameters (prevalence, mean intensity, diversity and similarity) were calculated by APL programs written by Mr. N. Weimer. Statistical calculations were made using formulae in Sokal and Rolfe (1981) and Siegel (1956).

D. Results

Description of the Communities

All 91 grebes examined were infected by two to fifteen species of intestinal helminths. A total of 34 species of helminths was found. Their prevalences and mean intensities in each species of grebe are listed in Table 2.

The fauna was dominated by cestodes (23 species, 96% of the individual worms). Two families were particularly significant, the Hymenolepididae with 13 species (*Dubininolepis* through *Echinatrium* in Table 2) and the Amabiliidae with five (the genera *Tatria* and *Schistotaenia*). Trematodes represented the second largest group of parasites (7 species, 3.4% of individuals). Nematodes were represented in grebes by only two species and 0.5% of the individuals. Acanthocephalans were rare; they were represented by two species and less than 0.01% of the individuals.

The general characteristics of the parasite communities in grebes are summarized in Table 3. More species of parasites were found in *Podiceps nigricollis* and *P.*

Table 2. Prevalences and mean intensities of intestinal helminths in four species of grebes collected in Alberta.

	Aechmophorus occidentalis (*n* = 20)		*Podiceps grisegena* (*n* = 33)		*Podiceps nigricollis* (*n* = 31)		*Podiceps auritus* (*n* = 7)	
	%[1]	$\bar{x}$[2]	%	$\bar{x}$	%	$\bar{x}$	%	$\bar{x}$
Trematoda								
Tylodelphys podicipina[a]	75	67	91	179	6	2		
Apatemon gracilis[b]	25	47	15	2	29	15	14	1
Cotylurus sp.[b]			3	1				
immature strigeids[c]			27	4				
Trichobilharzia sp.[c]					3	1		
Petasiger nitidus[a]	80	115	94	1025	16	44	43	131
Maritrema japonicum[b,d]			15	6				
Cestoda								
Schistocephalus solidus[b]	30	6	39	49	10	2		
Ligula intestinalis[b]	80	8	30	28	3	4	14	1
Tetrabothrius immerinus[b,d]	40	3	12	7			43	2
Dioecocestus asper[a]			73	2				
Tatria biremis[a]	30	5	85	377	100	2794	100	1616
Tatria decacantha[a]	5	1	82	1085	84	53	29	13

Table 2. continued

	Aechmophorus occidentalis		*Podiceps grisegena*		*Podiceps nigricollis*		*Podiceps auritus*	
	%	$\bar{x}$	%	$\bar{x}$	%	$\bar{x}$	%	$\bar{x}$
Schistotaenia colymba[a]					52	7	14	2
Schistotaenia tenuicirrus[a]			3	1				
Schistotaenia srivastavai[a]			73	18	6	2	43	6
Lateriporus skrjabini[c]					13	295		
Dubininolepis furcifera[a]	90	332	97	109	23	61	57	32
Dubininolepis podicipina[a]	5	10			94	65	14	5
Wardium paraporale[a]	100	25	94	113	100	1183	100	210
Pararetinometra lateralacantha[a]	5	2	18	56	13	11		
Parafimbriaria websteri[a]					6	3		
Nadejdolepis sp.[a]					48	883		
Diorchis sp. O[a]			3	3	84	220	43	6
Diorchis sp. P[a]	10	2			84	1635	14	23
Retinometra sp. A[a]			3	1				
Microsomacanthus sp. T[c]					16	58		
Microsomacanthus sp. W[c]					3	12		
Microsomacanthus sp. Z[c]					10	19		
Echinatrium sp. Y[c]					6	19		

Table 2. continued

	Aechmophorus occidentalis		Podiceps grisegena		Podiceps nigricollis		Podiceps auritus	
	%	$\bar{x}$	%	$\bar{x}$	%	$\bar{x}$	%	$\bar{x}$
Acanthocephala								
Polymorphus marilis[c]	10	2	3	6	3	10		
Corynosoma constrictum[b]			12	2				
Nematoda								
Capillaria obsignata[b]	40	3	88	21	39	5	43	3
Contracaecum ovale[b]	5	1	79	21	35	4	57	4

1- Percent of birds infected
2- Mean number of worms per infected bird
a- Grebe specialist
b- Generalist that matured in grebes
c- Did not mature
d- Has a marine life cycle

Table 3. General characteristics of the intestinal helminth communities in four species of grebes from Alberta, Canada.

	Aechmophorus occidentalis (*n* = 20)	*Podiceps grisegena* (*n* = 33)	*Podiceps nigricollis* (*n* = 31)	*Podiceps auritus* (*n* = 7)
Number of Lakes Sampled	3	5	6	2
Total No. of Parasite Species	16	23	26	14
Mean No. Species/Bird(SD)	6.4(1.7)	10.7(2.1)	9.1(2.3)	6.7(2.1)
Range in No. of Species	4-10	4-14	2-15	4-8
ln Mean No. Worms/Bird(SD)	5.9(0.8)	7.5(0.8)	8.2(1.1)	7.5(1.4)
Range in No. of Worms	112-1800	326-10459	231-33169	212-10943
Mean Diversity[1](SD)	.45(.21)	.57(.16)	.48(.20)	.24(.14)
Mean Jaccard Similarity(SD)	.40(.13)	.39(.14)	.41(.14)	.52(.13)
Mean Percent Similarity(SD)	56(22)	41(22)	56(22)	85(8)

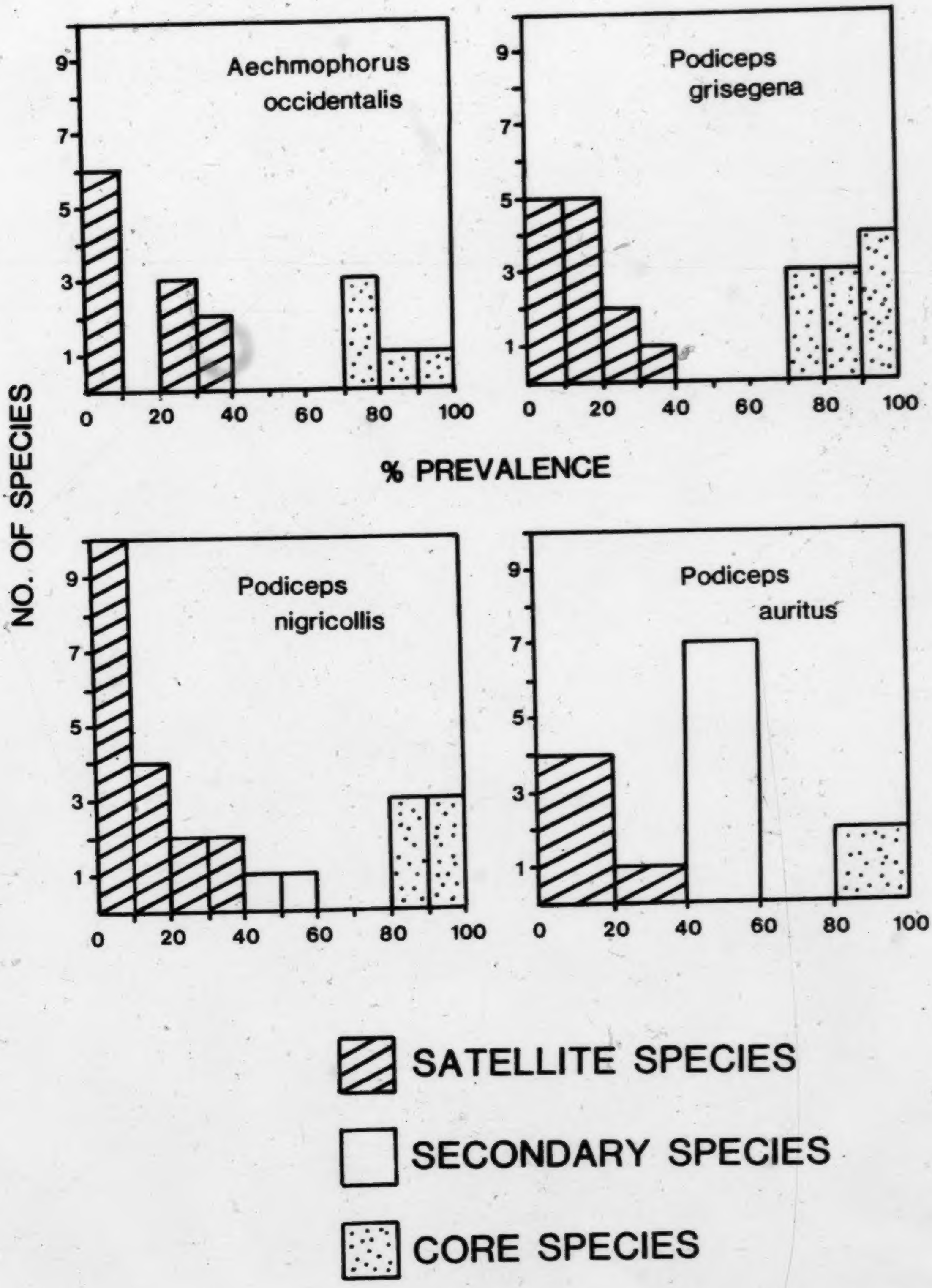
[1] Simpson's Index = $1 - \Sigma P_i^2$, where P_i is the proportion of species i.

grisegena than in the other grebes, in part because more were examined. However, species richness per bird was also higher for these hosts. *P. nigricollis* had the highest average worm burden and *A. occidentalis* the lowest. However, variance in this measure was high and there was considerable overlap among species. The helminth infracommunities in *P. grisegena* had the highest average diversity and the lowest average similarity among birds whereas those in *P. auritus* had the lowest average diversity and the highest average similarity.

Patterns of Association Among Helminth Species

Hanski's (1982) core/satellite hypothesis assumes that the frequency distributions of component species are bimodal and that frequent species are also locally abundant. Frequency distributions of the prevalences of the helminth species in each species of grebe, except *P. auritus*, were bimodal (Fig. 2). The relationship between frequency of parasite occurrence (here, prevalence) and local abundance (intensity) was positive and significant in each species of grebe (Kendall's rank correlation; $P<.05$ for *A. occidentalis* and *P. grisegena*, $<.01$ for *P. auritus* and $<.001$ for *P. nigricollis*). Since the assumptions were met, parasite species in the right-hand modes in Figure 2 (prevalence >70%) are regarded as core species, those in the left-hand mode (prevalence <40%) are regarded as satellite species, and species intermediate in prevalence are regarded as

Figure 2. Frequency distributions of prevalences of intestinal helminths in four species of grebes.


NO. OF SPECIES
% PREVALENCE
Aechmophorus occidentalis
Podiceps grisegena
Podiceps nigricollis
Podiceps auritus
1
3
5
7
9
0
20
40
60
80
100
SATELLITE SPECIES
SECONDARY SPECIES
CORE SPECIES

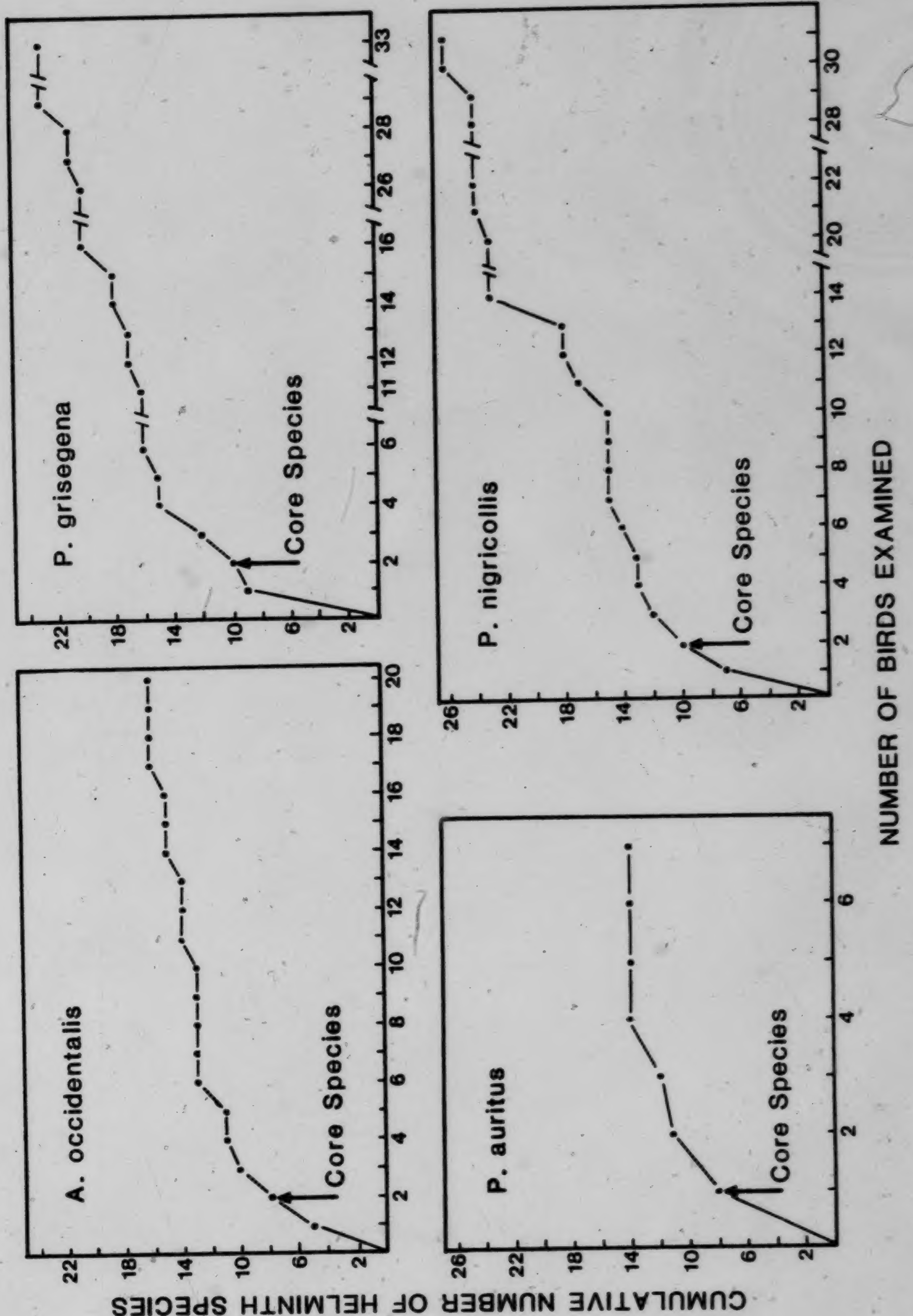
secondary species (as in Bush and Holmes, MS). The same prevalence criteria were used to identify core, secondary and satellite species in *P. auritus*.

P. grisegena had the largest number of core species, ten (=31% of the community), while *P. auritus* had the smallest number, two (14%). Fourteen of the parasite species were identified as core species in one or more of the grebe species; most (11) are specialists of grebes. Specialists are defined here as species that are reported solely from grebes or mature only in grebes. The other three species, *Ligula intestinalis*, *Capillaria obsignata* and *Contracaecum ovale* are host generalists, having been reported from many species of birds and mammals. *Wardium paraporale* was a core species in all four species of grebes, *Tatria biremis* was a core species in all three species of *Podiceps*, and four other helminths were core species in at least two grebe species (Table 4). Twelve of the 14 core species have satellite status in one or more of the other species of grebes. The two exceptions are *W. paraporale*, a core species in all four grebes, and *Dioecocestus asper*, found exclusively in *P. grisegena*. The largest of the *Podiceps* grebes, *P. grisegena*, shared four core species with the large, fish-eating *A. occidentalis*, and three core species with the smaller, mainly invertebrate-eating grebes. All core species in all four species of grebes were recovered after examination of only two individual birds of each host (Fig. 3)

Table 4. Associations of some helminths in four species of grebes using recurrent group, core/satellite and cluster analyses. Ao = *Aechmophorus occidentalis*, Pg = *Podiceps grisegena*, Pn = *Podiceps nigricollis*, Pa = *Podiceps auritus*. C = core, 2 = secondary, S = satellite, r = recurrent group member, a = associate species. * = main host (see text for definitions).

	Recurrent Group		Grebe Specialist	Ao	Pg	Pn	Pa	Cluster
	A	B						
Dubininolepis podicipina		X	X	S		C*r		3
Schistotaenia colymba		X	X			2 r	S	3
Nadejdolepis sp.		X	X			2 a		3
Diorchis sp. O	a	X	X		S	C*r	2	3
Diorchis sp. P	a	X	X	S		C*r	S	3
Tatria biremis	X	a	X	S	C r	C*r	C r	3
Tatria decacantha	X	a	X	S	C*r	C r	S a	1
Wardium paraporale	X		X	C r	C r	C*r	C r	3
Petasiger nitidus	X		X	C r	C*r	S	2 a	2
Dubininolepis furcifera	X		X	C*r	C r	S	2 r	1
Capillaria obsignata	X			S a	C*r	S a	2	1
Contracaecum ovale	X			S	C*r	S r	2 r	1
Tylodelphys podicipina	a		X	C r	C*r	S		2
Dioecocestus asper	a		X		C*r			1
Schistotaenia srivastavai	a		X		C*r	S	2	1
Schistocephalus solidus				S a	S a	S		1
Tetrabothrius immerinus				S a			2 a	2
Ligula intestinalis				C*r	S	S	S	
Schistotaenia tenuicirrus			X		S			
Pararetinometra lateralacantha			X	S	S	S		1
Parafimbriaria websteri			X			S		

Figure 3. The cumulative number of helminth species found as a function of the number of birds examined. Individual birds are arranged in the order in which they were examined. Arrows indicate the number of birds that were examined before all core helminth species had been recovered.


A. occidentalis
P. grisegena
P. auritus
P. nigricollis
Core Species
Core Species
Core Species
Core Species
CUMULATIVE NUMBER OF HELMINTH SPECIES
NUMBER OF BIRDS EXAMINED
2
6
10
14
18
22
26
2
4
6
8
10
11
12
14
16
18
20
22
26
28
30
33

Secondary species were rare in the helminth communities of grebes. *A. occidentalis* and *P. grisegena* had none, while only two (*Schistotaenia colymba* and *Nadejdolepis* sp., both grebe specialists) of the 26 parasites infecting *P. nigricollis* were in this category. However, secondary species made up the largest proportion of the community in *P. auritus* (7 of 14 species). Six were core species in other grebes, five in *P. grisegena*, one in *P. nigricollis*; the other, *Tetrabothrius immerinus*, is a cestode with a known marine life cycle which infects marine mammals and fish-eating birds (Baer, 1954).

The communities in *P. nigricollis* and *A. occidentalis* had the largest proportion of satellite species (69% in each). Satellite species were frequently core or secondary species in another species of grebe (20 of 42 host-parasite combinations) (Table 4) or in another type of host found in the same habitat (for example, *Polymorphus marilis* is a core species in lesser scaup, Bush and Holmes, MS).

Patterns in the way individual species of helminths associate in individual birds were examined using recurrent group analysis. Recurrent group analysis (Fager, 1957; Fager and McGowan, 1963; Fager and Longhurst, 1968; Bush, 1980) identifies groups of species that regularly co-occur in the same birds. It is based on the calculation of an index of affinity which is the geometric mean of the proportion of joint occurrences, corrected for sample size. Associations are dichotomized into those that are significantly positive (see Fager and McGowan, 1963 for definition), and those that are not. The largest groups of species in which each species is positively associated with all others are the recurrent groups; such groups can be shown graphically by interconnections with thick lines (Fig. 3). The position of each species in the graph is arbitrary. Species that form positive associations with some, but not all, of the recurrent group members are designated as associate species (their associations are depicted in the graph by thin lines).

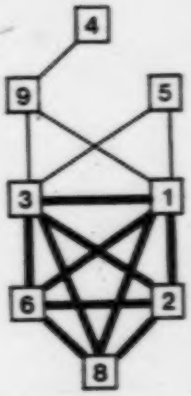
The analysis was applied to the data from each species of grebe separately, then to the combined data from all grebes regardless of species. Each species of grebe had a single recurrent group; the complexity ranged from that in *P. auritus* (four species, plus three associates) to that in *P. grisegena* (ten species plus a single associate species). In each host species, all core species were members of the recurrent group; additional species were included in the recurrent groups of *P. auritus* and *P. nigricollis*. These additional species and the associate species for all four grebes included some satellite species (Table 4).

The combined analysis revealed two recurrent groups with no species in common. However, two members of each group were associates of the other group (Fig. 5). The larger recurrent group (Group A) was composed of seven species, with links to five associate species. This recurrent group is composed of species that were part of the

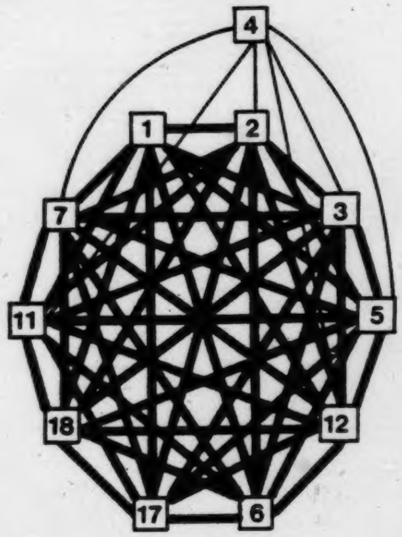
Figure 4. Diagrammatic summary of recurrent group analysis to identify groups of parasite species that regularly co-occurred in four species of grebes (Western grebes, *Aechmophorus occidentalis*; Red-necked grebes, *Podiceps grisegena*; Eared grebes, *Podiceps nigricollis*; and Horned grebes, *Podiceps auritus*).

Recurrent groups are connected by thick lines, associate species by thin lines (see text).

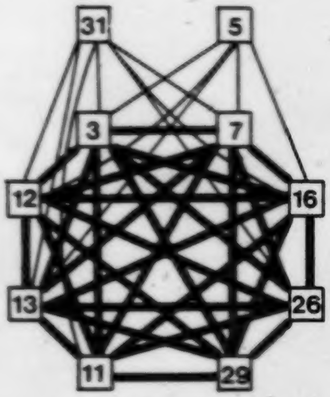
Numbers refer to helminth species: 1= *Dubininolepis furcifera*; 2= *Petasiger nitidus*; 3= *Wardium paraporale*; 4= *Schistocephalus solidus*; 5= *Capillaria obsignata*; 6= *Tylodelphys podicipina*; 7= *Tatria biremis*; 8= *Ligula intestinalis*; 9= *Tetrabothrius immerinus*; 11= *Contracaecum ovale*; 12= *Tatria decacantha*;
13= *Diorchis* sp. P; 16= *Dubininolepis podicipina*;
17= *Dioecocestus asper*; 18= *Schistotaenia srivastavai*;
26= *Diorchis* sp. O; 29= *Schistotaenia colymba*;
31= *Nadejdolepis* sp.



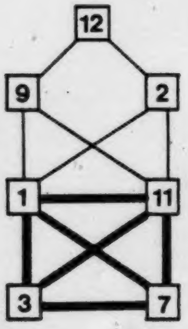
A. occidentalis



P. grisegena

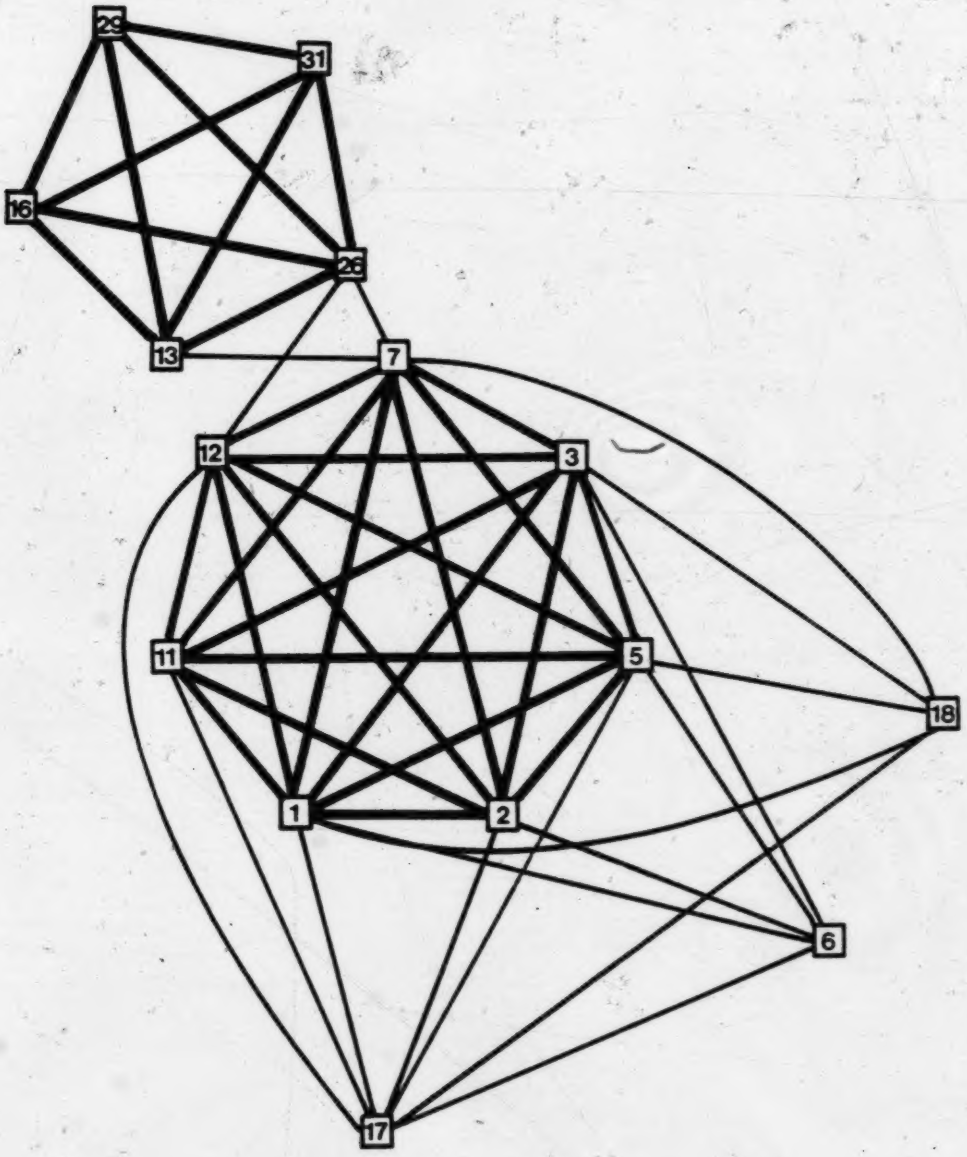


P. nigricollis



P. auritus

Figure 5. Recurrent group (thick lines) and associate (thin lines) species in 91 grebes of four species. Numbers refer to helminth species: 1= *Dubininolepis furcifera*; 2= *Petasiger nitidus*; 3= *Wardium paraporale*; 5= *Capillaria obsignata*; 6= *Tylodelphys podicipina*; 7= *Tatria biremis*; 11= *Contracaecum ovale*; 12= *Tatria decacantha*; 13= *Diorchis* sp.P; 16= *Dubininolepis podicipina*; 17= *Dioecocestus asper*; 18= *Schistotaenia srivastavai*; 26= *Diorchis* sp.O; 29= *Schistotaenia colymba*; 31= *Nadejdolepis* sp.



recurrent group in *P. grisegena* and also in the recurrent group (or accessory species) in two or more of the other species of grebes. Three associates, not including those in Group B, are members of the recurrent group of *P. grisegena*; of these three, only *Tylodelphys podicipina* is a member of a recurrent group in another grebe (*A. occidentalis*). Of the seven helminths in Group A, five are specialists of Podicipediformes (Table 4). Only *Contracaecum ovale* and *Capillaria obsignata* are generalists. All five associate species of Group A are grebe specialists.

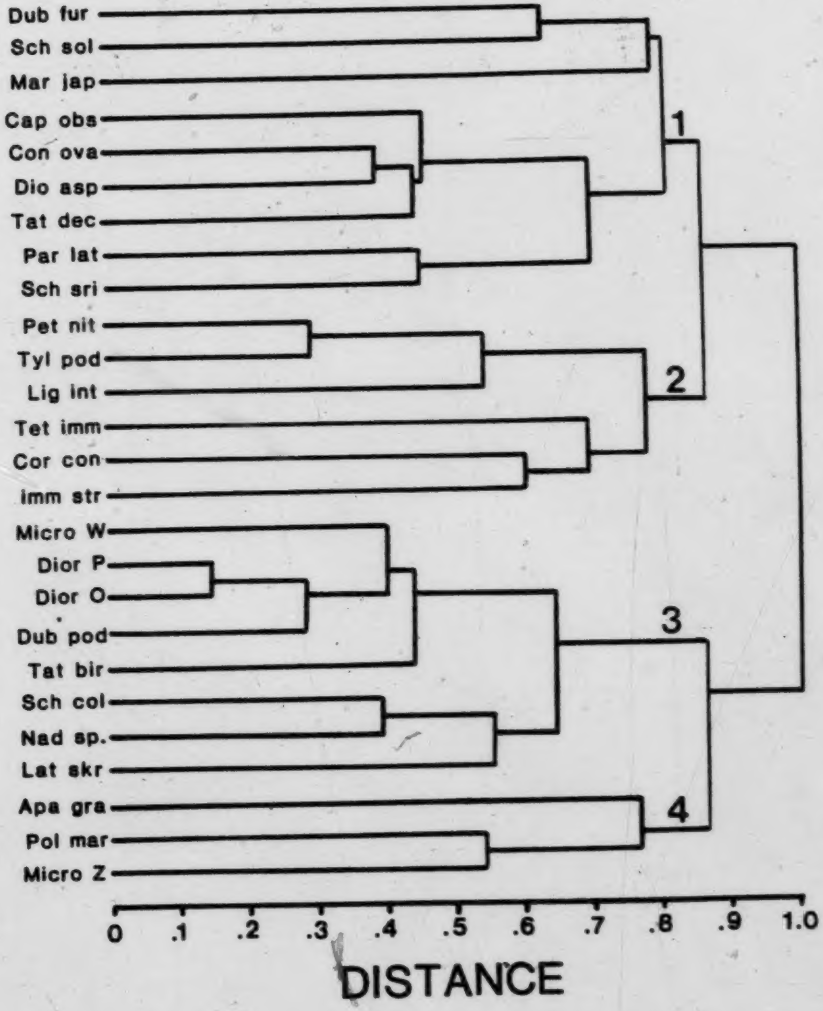
The smaller recurrent group (Group B), is composed of five species; four are members of the recurrent group and the other is an associate species in *P. nigricollis*; none are in the recurrent groups (or associates) in any of the other hosts. All five are grebe specialists. The two associate species of Group B (both members of Group A), are species that are common in both *P. nigricollis* and *P. grisegena*.

Evidence for robust structure within the helminth infracommunities in each species of grebe was shown by considering ranked abundances of the members of the recurrent group in each individual grebe. In all cases, Kendall's index of concordance (W) was high and statistically significant (*A. occidentalis*: $W=.672, P<.005$; *P. grisegena*: $W=.669, P<.005$; *P. nigricollis*: $W=.839, P<.005$; *P. auritus*: $W=1.0, P<.005$). Members of each recurrent group not only frequently co-occur, but also maintain similar relative abundance relationships in all individuals of that species of grebe.

Despite the fact that many parasite species were shared among grebes, the bulk of the breeding population for each species was often maintained in only one host. This host has been called the main or required host (Holmes *et al.*, 1977). For example, *Tatria decacantha* occurred in all four host species, but 95% of the population occurred in *P. grisegena* (Table 2). Therefore, *P. grisegena* was considered the main host for *T. decacantha*. Main hosts are designated by asterisks in Table 4.

Patterns of similarity in the distribution of worms across individuals of all four species of grebes were examined using cluster analysis. Species of parasites found in three or fewer birds were disregarded, leaving 26 species of helminths in the analysis. A hierarchial clustering analysis was performed on presence/absence data, using the Jaccard similarity measure and the average distance algorithm (Fox and Guire, 1976). Clustering by variable (*i.e.*, parasite species) resulted in a dendrogram in which four groups can be distinguished (Fig. 6). Only one of these, Cluster 3, was reasonably well-defined; it contained all of the species in recurrent Group B, plus *Wardium paraporale* and *Tatria biremis*, species that were widely distributed across grebes, but reached their highest mean intensities in *P. nigricollis*. Cluster 1, especially the lower of the two subclusters, included species common in *P.*

Figure 6. Cluster dendrogram of intestinal helminths of 91 grebes of four species based on presence/absence data, using the average distance algorithm and the Jaccard similarity measure. (Parasites had to occur in more than three birds to be included. Refer to Table 2 for identities of helminth species).


Dub fur
Sch sol
Mar jap
Cap obs
Con ova
Dio asp
Tat dec
Par lat
Sch sri
Pet nit
Tyl pod
Lig int
Tet imm
Cor con
imm str
Micro W
Dior P
Dior O
Dub pod
Tat bir
Sch col
Nad sp.
Lat skr
Apa gra
Pol mar
Micro Z
1
2
3
4
0
.1
.2
.3
.4
.5
.6
.7
.8
.9
1.0
DISTANCE

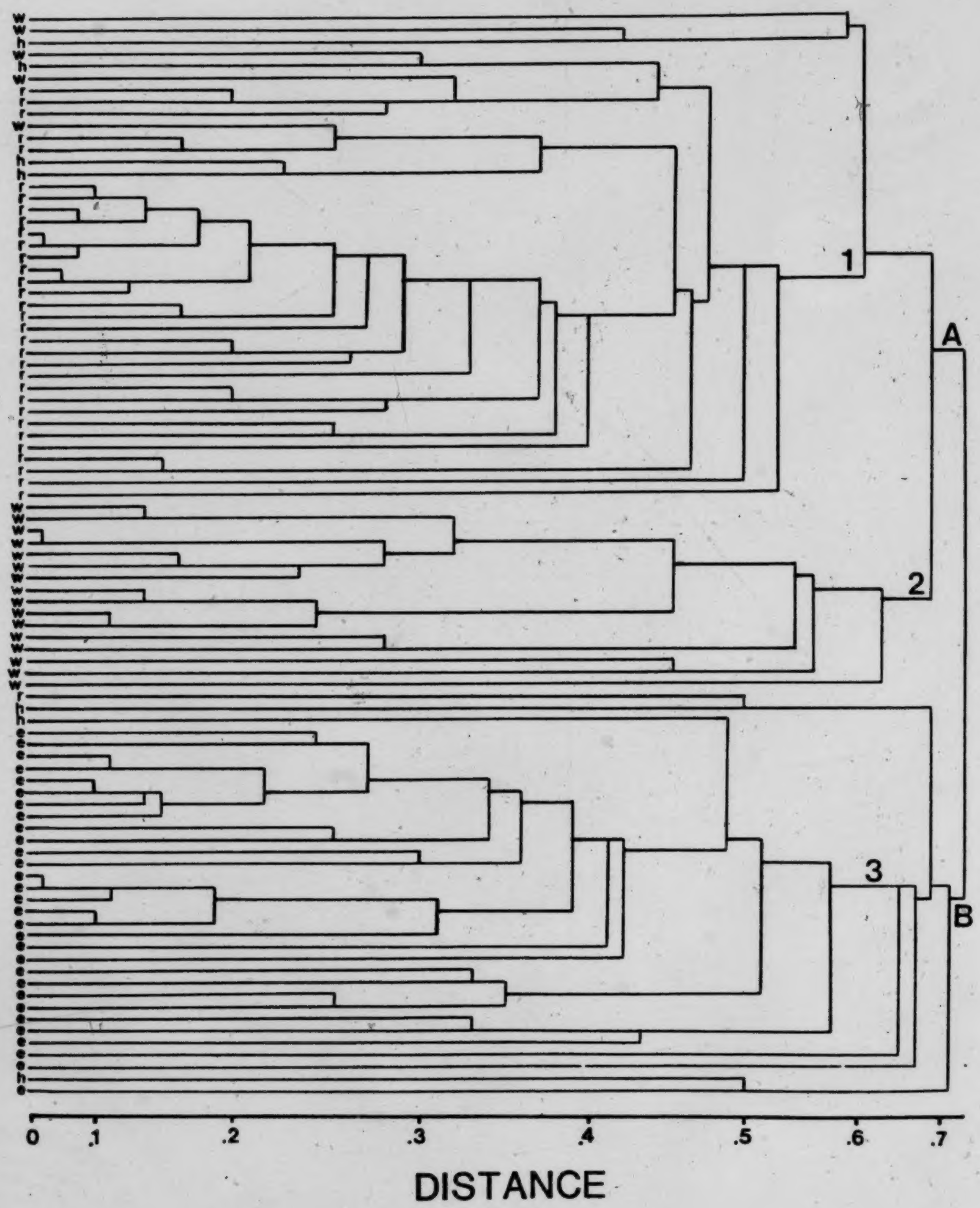
grisegena and *P. auritus*. Cluster 2 was a loose association of those helminths common in large grebes, particularly those utilizing fish as intermediate hosts. Cluster 4 was composed of species not common in any species of grebe.

Patterns of Similarity Among Infracommunities

Three methods, clustering with presence/absence data, clustering using the numbers of worms, and principal components analysis, were used to assess patterns of similarity among infracommunities. The dendrogram based on the Jaccard presence/absence measure (Fig. 7) exhibited two major groups (A and B) comprising three well-defined clusters (1,2 and 3), plus 9 individual infracommunities that were isolated or formed small groups. Group A contained all but one of the individuals of the larger, fish-eating grebes (*A. occidentalis* and *P. grisegena*), while group B contained most of the smaller, largely invertebrate-eating birds (all of the *P. nigricollis* and 3 of 7 *P. auritus*).

Clusters 1, 2, and 3 correspond essentially to three single-host species clusters. Cluster 1 contained 32 of 33 *P. grisegena* (plus 3 *A. occidentalis* and 2 *P. auritus*). Cluster 2 had 15 of 20 *A. occidentalis* and Cluster 3 contained 28 of 31 *P. nigricollis* (plus a single *P. auritus*). Individuals of *P. auritus* were widely scattered among the three major clusters and the isolated small groups.

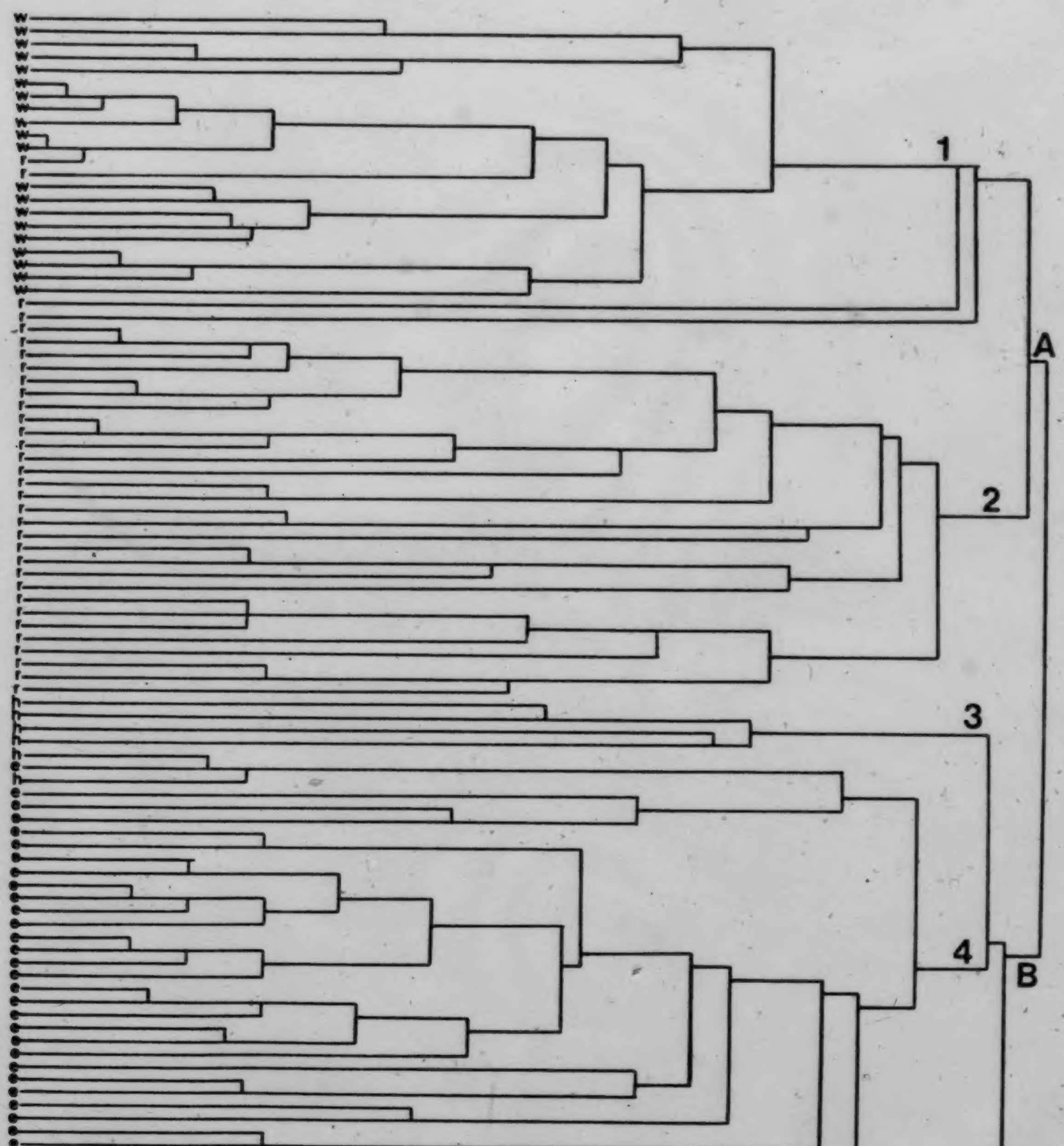
Figure 7. Cluster dendrogram of 91 grebes of four species based on the presence/absence of intestinal helminths, using the average distance algorithm and the Jaccard similarity measure. w = Aechmophorus occidentalis, r = Podiceps grisegena, e = Podiceps nigricollis, h = Podiceps auritus. (Major clusters A and B, and subclusters 1,2, and 3 are discussed in text).


1
A
2
3
B
0
.1
.2
.3
.4
.5
.6
.7
DISTANCE

Second, patterns in the distribution of numbers of worms among infracommunities were assessed by a similar cluster analysis, using the average distance on ln(x+1) transformed and standardized data (number of worms in each bird). The distance measure used was the complement of the product-moment correlation coefficient (for further details see Fox and Guire, 1976). The resultant dendrogram (Fig. 8) showed the same basic patterns as the analysis of presence/absence data, but more clearly. The two largest groups separated all of the large grebes from all of the smaller ones. All *A. occidentalis* (plus 2 *P. grisegena*) were in Cluster 1, 29 of 33 *P. grisegena* were in Cluster 2, four of seven *P. auritus* were in Cluster 3 and 30 of 31 *P. nigricollis* (plus two *P. auritus*) were in Cluster 4. There were only two small secondary clusters, one (containing two *P. grisegena*) associated with Cluster 1, the other (containing one *P. nigricollis* and one *P. auritus*) associated with Clusters 3 and 4. There was no significant trend for birds to cluster by sex, year of capture, date of capture, or lake of residence.

The third method used to assess patterns was principal components analysis (PCA). Unlike cluster analysis, PCA does not force groupings where none exist in the data. PCA was performed on the entire 91 bird sample using ln(x+1) transformed abundances of the 34 helminth species as attributes. Using the covariance matrix, the first two principal components accounted for 61% of the variance; the

Figure 8. Cluster dendrogram of 91 grebes of four species based on ln (x + 1) transformed intensities of intestinal helminths, using the average distance algorithm and the complement of the product-moment correlation coefficient as the distance measure. w = *Aechmophorus occidentalis*, r = *Podiceps grisegena*, e = *Podiceps nigricollis*, h = *Podiceps auritus*. (Major clusters A and B, and subclusters 1 to 4 are discussed in text).


1
A
2
3
4
B
0
.1
.2
.3
.4
.5
.6
.7
.8
.9
1.0
DISTANCE

third component accounted for only 7% more (Table 5). A plot of the scores of PC1 and PC2 demonstrated a pattern similar to that noted from cluster analysis, namely, four clouds of points corresponding to the grebe species (Fig. 9). PC1 separated communities from large and small grebes while PC2 separated *A. occidentalis* from *P. grisegena*. Communities from *P. auritus* overlapped those from both *P. nigricollis* and *P. grisegena*.

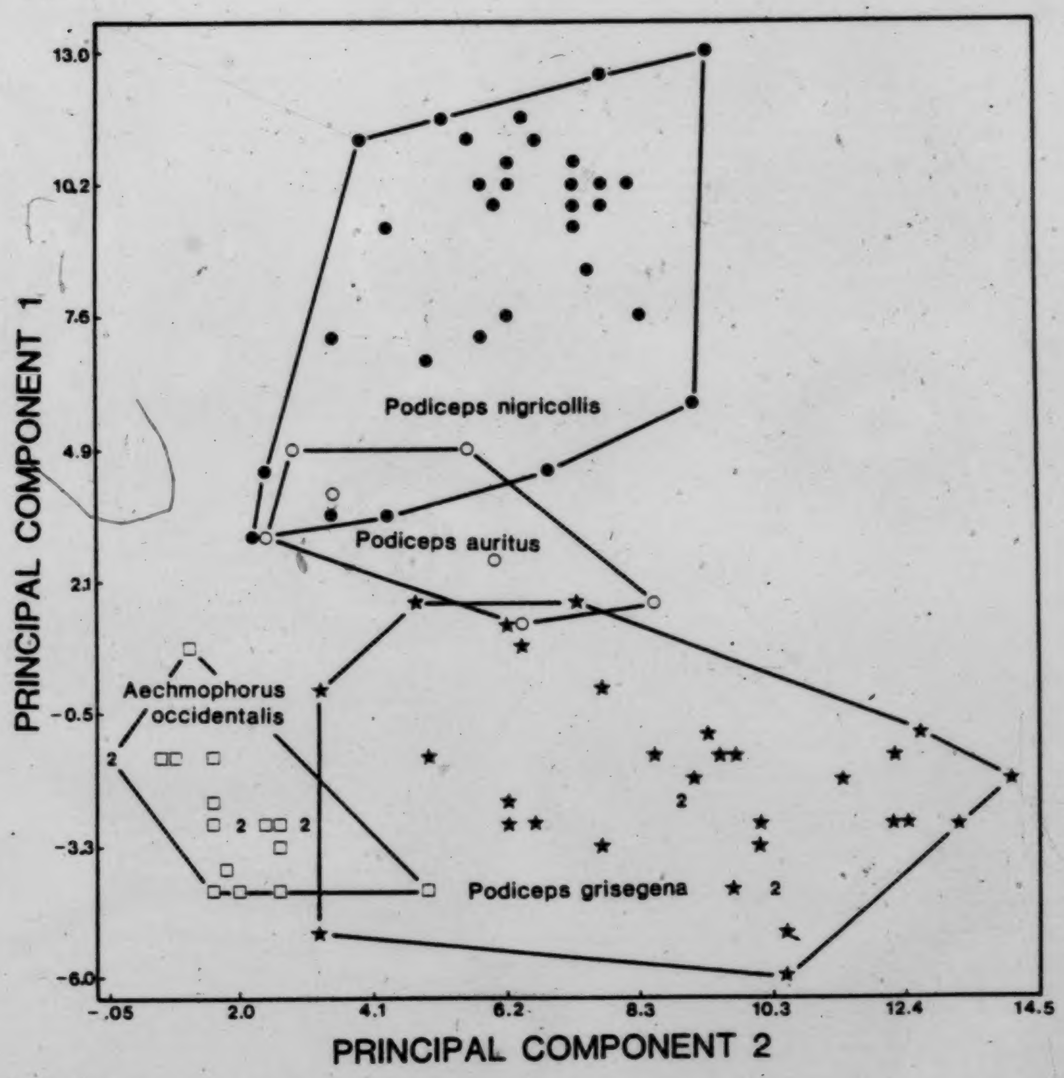
Inspection of coefficients of the first three components suggested that three species of parasites, *Petasiger nitidus*, *Tylodelphys podicipina* and *Tatria biremis* were particularly important variables. *Diorchis* species "P" and "O", and *Dubininolepis podicipina*, all core species of *P. nigricollis* were also important in PC1, with *Tatria decacantha* important in PC2 and *Dubininolepis furcifera* in PC3. These species are all specialists of the Podicipediformes.

These analyses indicated that at least three of the four hosts, *A. occidentalis*, *P. grisegena*, and *P. nigricollis*, had distinctive helminth faunas. There was also a clear distinction between the parasite faunas of large and small species of grebes. They also suggest that both the species of parasites present and the relative abundances of shared species are important in delimiting these characteristic faunas.

Table 5. Amount of Variance Explained and Coefficients of the First Three Principal Components of the Covariance Matrix using the ln(x+1) transformed abundances of 34 Helminth Parasites of Four Species of Grebes, Podicipediformes, from Alberta.

	PC 1	PC 2	PC 3
Component	31.29	11.27	5.18
Variance Explained (%)	44.66	60.73	68.12
Dubininolepis furcifera	-.277	-.098	-.435
Petasiger nitidus	-.386	.467	.240
Wardium paraporale	.227	.137	.052
Schistocephalus solidus	-.057	.070	-.158
Capillaria obsignata	-.076	.241	-.024
Tylodelphys podicipina	-.286	.123	.387
Tatria biremis	.436	.343	-.513
Ligula intestinalis	-.090	-.101	.243
Tetrabothrius immerinus	-.033	.014	.008
Apatemon gracilis	.019	-.035	.029
Contracaecum ovale	-.046	.266	-.086
Tatria decacantha	.141	.664	.042
Diorchis sp. P	.485	.045	.324
Pararetinometra lateralacantha	-.022	.086	.0003
Polymorphus marilis	.003	-.001	.007
Dubininolepis podicipina	.257	.004	.134
Dioecocestus asper	-.039	.090	-.047
Schistotaenia srivastavai	-.049	.105	-.177
Maritrema japonicum	-.024	.046	-.050
Corynosoma constrictum	-.009	.015	.006
immature strigeids	-.021	.033	.024
Schistotaenia tenuicirrus	-.001	.003	.0000
Retinometra sp. A	-.001	.001	.003
Diorchis sp. O	.300	.017	.200
Cotylurus sp.	-.001	.005	-.003
Schistotaenia colymba	.062	.024	.047
Lateriporus skrjabini	.035	.012	.037
Nadejdolepis sp.	.166	.039	.193
Parafimbriaria websteri	.003	-.005	-.012
Microsomacanthus sp. T	.042	.011	.037
Echinatrium sp. Y	.017	.003	.014
Microsomacanthus sp. W	.009	.0007	.007
Microsomacanthus sp. Z	.029	.008	.024
Trichobilharzia sp.	.002	.0000	.002

Figure 9. Distribution of 91 grebes of four species in principal components space, using principal components 1 and 2 of the covariance matrix.



13.0
10.2
7.6
4.9
2.1
-0.5
-3.3
-6.0
PRINCIPAL COMPONENT 1
-.05
2.0
4.1
6.2
8.3
10.3
12.4
14.5
PRINCIPAL COMPONENT 2
Podiceps nigricollis
Podiceps auritus
Aechmophorus occidentalis
Podiceps grisegena
2

E. Discussion

Host specificity makes an important contribution to intestinal helminth community structure in grebes. Half of all species found, and 11 of 14 of those that occurred in more than 70% of the birds, mature only in grebes. Only one species, *Dioecocestus asper*, was specific to one species of host, *Podiceps grisegena*. Most other parasites occurred in several host species, but the bulk of adult specimens were maintained in only one species of host.

Helminth communities in three grebe species, *Aechmophorus occidentalis*, *Podiceps grisegena* and *P. nigricollis* had species frequency distributions that were strongly bimodal. Each had a substantial number of frequent core species, most of which occurred in large numbers. Recurrent group analysis showed that these species (or a slightly larger number in *P. nigricollis*) regularly co-occurred. Although the majority of the core species are specific to grebes, a small proportion are wide ranging host generalists, at least two of which (*Ligula intestinalis* and *Contracaecum ovale*) use fish as intermediate hosts and mature rapidly in a wide variety of homeotherms (Dubinina, 1964; Rysavy and Ryzhikov, 1978). Overall, the core-satellite species hypothesis of Hanski (1982) provided a good description of the patterns of association of parasites in grebes.

As a result of the bimodal species frequencies and the contribution of host specificity, both cluster and principal

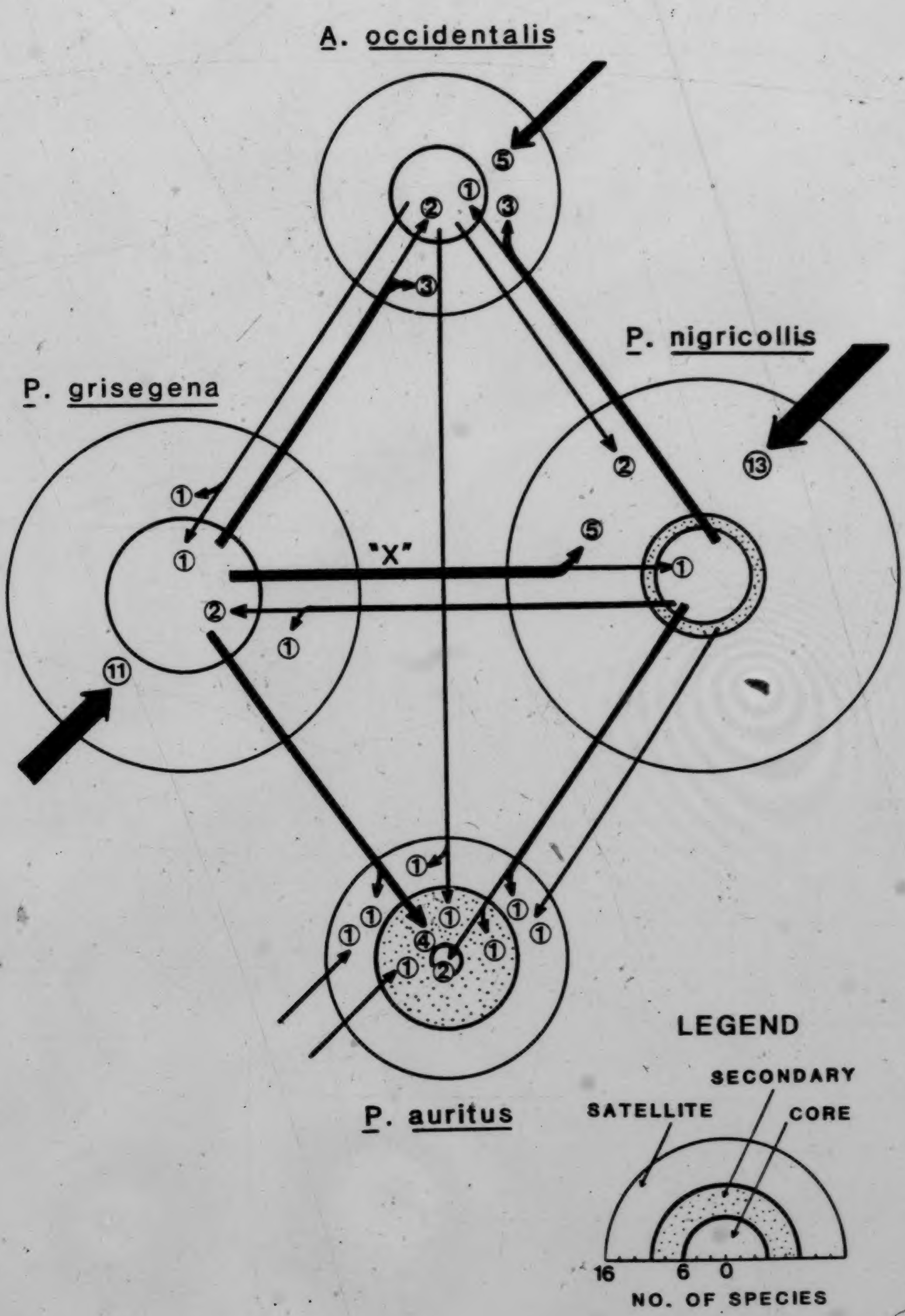
1

components analyses identified characteristic parasite communities in *A. occidentalis*, *P. grisegena*, and *P. nigricollis*. Each of these communities contained a central block of core species that conferred much similarity among the infracommunities of each host species. Each community had at least one core species that was not a core species in any other grebe, and each had a fauna characterized by differential abundances of co-occurring species.

Individuals of *Podiceps auritus*, however, displayed a less characteristic helminth community that was essentially a composite of those in *P. grisegena* and *P. nigricollis*. *P. auritus* had only two core species and four recurrent group species, all of which were more abundant in other grebes. Because *P. auritus* are usually residents of ponds, sloughs and potholes, rather than lakes (Faaborg, 1976; Ferguson, 1981), the birds that I sampled may not have had their typical helminth fauna. However, competition for nesting sites and use of the same food with *P. grisegena* (Fjeldsa, 1973; 1983) may result in only subtle differences in the helminth faunas, not detectable with the small sample size (7 *P. auritus*) available.

In addition to the core species element, each community examined had a number of satellite species. The sources of these are shown in Figure 10, which demonstrates patterns of exchange of helminths among the four species of grebes. A high proportion of the satellite species were core species in other grebes. A few satellites are generalists that

Figure10 . Patterns of exchange of intestinal helminth parasites among four species of grebes. Size of circles is proportional to the number of species in each community. Arrows represent direction of exchange, for example, arrow X indicates that six core species of _P. grisegena_ are shared with _P. nigricollis_, five as satellites and 1 as a core species.


A. occidentalis
⑤
①
②
③
③
P. nigricollis
P. grisegena
②
⑬
①
⑤
①
"X"
①
②
①
⑪
①
①
①
①
①
①
①
④
①
①
①
②
P. auritus
LEGEND
SECONDARY
SATELLITE
CORE
16
6
0
NO. OF SPECIES

mature in a variety of birds and mammals living in and around lakes; some are immature specimens, probably of species that mature in other water birds; and two are marine "relic" species that are acquired during the winter and persist for varying lengths of time during the breeding season while the birds are on fresh water. A small, but perplexing, element of the satellite (or secondary) species group were parasites that are thought to be grebe specialists, but were always found to be rare (*e.g.*, *Pararetinometra lateralacantha*, *Parafimbriaria websteri*). Some may be core species in the community of *Podilymbus podiceps*, which I did not examine. Others may be core species in *P. auritus* from ponds and sloughs, occurring only sporadically in the birds that were collected on lakes.

Cluster and principal components analyses also isolated the helminth communities of the large species of grebes, *A. occidentalis* and *P. grisegena*, from those of the smaller *P. nigricollis*. This probably reflects the differences in food habits of these species. The diet of *A. occidentalis* is fish, which are speared by the well-developed, needle-like bill. Individuals of *P. grisegena* also consume many fish. Both grebes had large numbers of helminths with fish intermediate hosts. They included the most abundant trematode species, *Tylodelphys podicipina* and *Petasiger nitidus*. *P. nigricollis* concentrates on invertebrates. Its helminth fauna was dominated by small hymenolepidid and amabiliid cestodes that use crustacea and odonates as intermediate hosts.

Gallimore (1964) examined helminths from grebes in Alberta. Using the prevalences of parasites he provided, after correcting some identifications based on examination of his specimens and taxonomic revisions since 1964, I was able to determine the proportion of core, secondary and satellite species (Table 6). As in this study, Gallimore found that the largest proportion of parasites in each host species was the satellite component. However, unlike the results of this study, Gallimore found a relatively large proportion of secondary species (except in *P. auritus*), and a maximum of 10% core species (in *A. occidentalis* and *P. auritus*). These differences may be attributable to two differences in procedures. First, Gallimore collected birds from a variety of habitats, including ponds and sloughs, whereas all birds in this study came from lakes; parasites may be more patchily distributed in the smaller habitat "islands". Second, the intestines of all birds in this study were flash-frozen quickly after death of hosts to preclude autolytic degeneration of delicate parasite specimens; Gallimore's were not. He kept birds intact, in a cool place, until he returned to the laboratory, where grebes were examined the same day or frozen, still intact, at -18°C. The experience in our lab (J.C. Holmes, pers. comm.) is that flash-freezing in the field results in intensities an order of magnitude higher, as well as much higher prevalences.

Table 6. A comparison of core, secondary and satellite species components of intestinal helminth communities in grebes and waterfowl.

Community	Study	Total No. of Species	%Core	%Secondary	%Satellite
Grebes					
Aechmophorus occidentalis	1	16	31	0	69
	2	9	10	20	70
Podiceps grisegena	1	23	43	0	57
	2	27	7	25	68
Podiceps nigricollis	1	26	23	8	69
	2	21	9	18	73
Podiceps auritus	1	16	14	50	36
	2	19	10	0	90
Waterfowl					
Aythya affinis	3	30	23	20	57
	4	52	15	12	73
Anas americana	5	17	6	29	65
Anas discors	5	31	13	19	68
Anas platyrhynchos	5	47	2	41	57
Anas strepera	5	24	21	50	29
Aythya collaris	5	20	5	30	65
Aythya valisineria	5	48	10	42	48
Bucephala albeola	5	22	0	32	68
Melanitta fusca	5	43	23	40	37
Oxyura jamaicensis	5	19	26	32	42

1 - This study
2 - Gallimore, 1964.
3 - Hair, 1975.
4 - Bush, 1980.
5 - Butterworth, 1982.

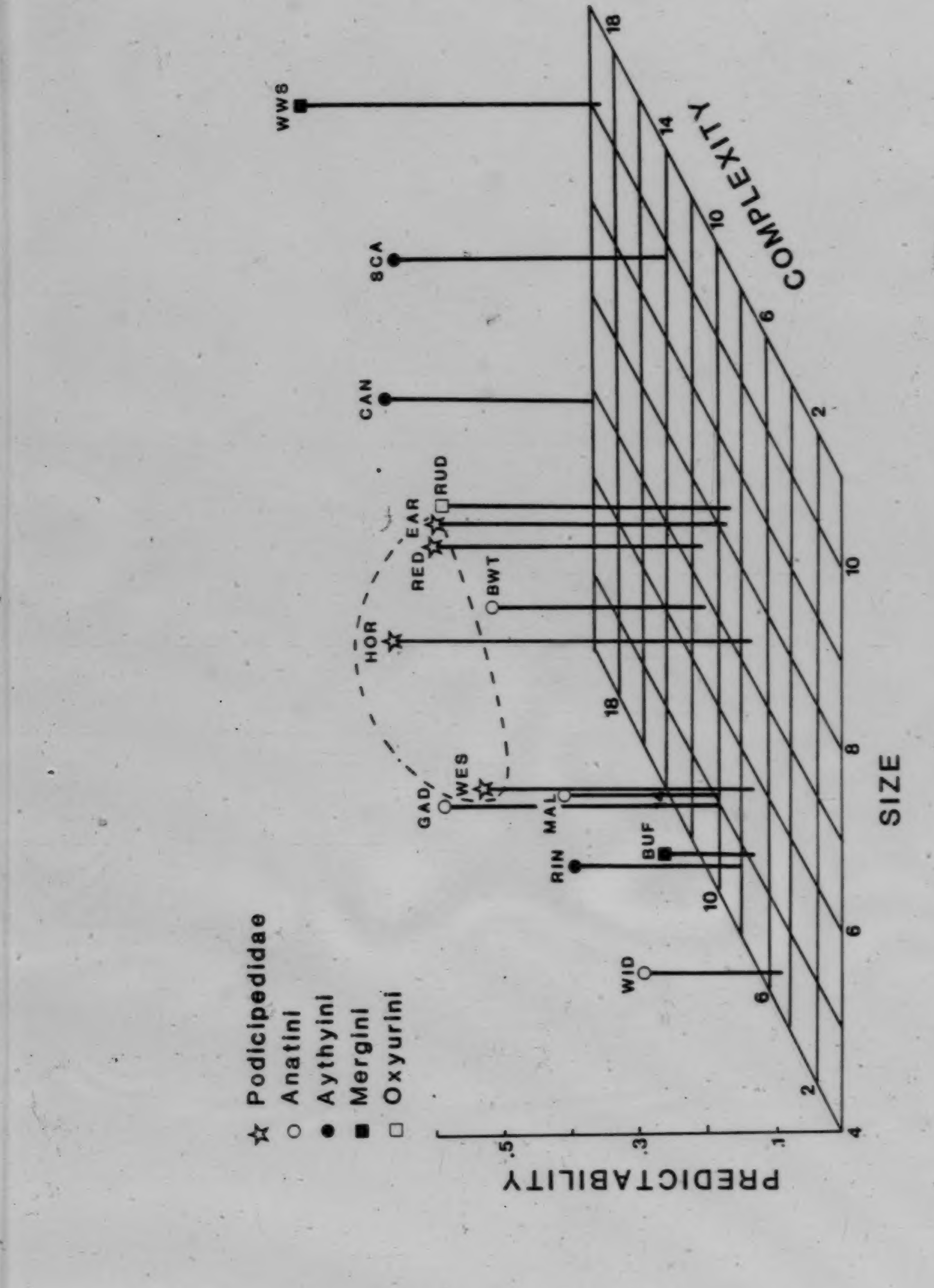
Using Gallimore's data, each of the *Podiceps* grebes had two core species; *A. occidentalis* had one. *Dubininolepis furcifera* was a core species in each of the *Podiceps* species and a secondary species in *A. occidentalis*. Both *P. nigricollis* and *P. auritus* had the same second core species, *Tatria biremis*; *P. grisegena* had *Schistotaenia srivastavai* as the second core species. *Wardium paraporale*, identified as *Dicranotaenia* sp. by Gallimore, was the lone core species in *A. occidentalis*. Besides Gallimore's study, no other complete parasitological surveys of grebes, that can be used for comparison, have been conducted.

Hair (1975) and Bush (1980), using the same procedures employed in this study, examined the helminth community of *Aythya affinis*. In both studies the community demonstrated a bimodal pattern of species frequencies, with the core element representing a larger proportion of the community than secondary species. Hair's study identified a greater proportion of the community as core species (23% *vs*. 15%), a level similar to that for *P. nigricollis*. As was noted for the communities in grebes, the satellite element of the community in *A. affinis* was the largest segment. Butterworth (1982) presented information on the helminth communities in nine additional species of waterfowl collected on several lakes in Alberta. In seven of the nine hosts, satellite species comprised the largest proportion of each community (Table 6). *Melanitta fusca* and *Anas strepera* had helminth communities with secondary species making up the largest component. Only three waterfowl species, *M. fusca*, *A. strepera* and *Oxyura jamaicensis*, had faunas with significant proportions of core species, approximately the same proportion that occurred in *P. nigricollis*. None of these studies, however, demonstrated communities with a core element that was as large a proportion of the communities as in *A. occidentalis* (31%) or *P. grisegena* (43%).

Butterworth (1982) plotted the helminth communities of ten species of waterfowl in three-dimensional space, using community size (mean number of worms per bird), complexity (mean number of species per bird), and similarity (mean Jaccard similarities between pairs of birds, termed predictability in Fig. 11) of infracommunities as attributes. He noted that the ducks showed a "loosely structured cline" of communities from those with low complexity, small size and low predictability (*e.g.*, *B. albeola* = BUF in Fig. 11 and *A. americana* = WID) to those with high complexity, large size and high predictability (*e.g.*, *A. affinis* = SCA and *M. fusca* = WWS). The communities of grebes are intermediate in size and complexity, but more predictable than those of the majority of communities from ducks that were similar in size and complexity (Fig. 11). This reflects the high proportion of core species as well as a smaller pool of parasite species with the potential to invade grebes.

In summary, the intestinal helminth communities in three of four grebes were predictably structured and

Figure 11. Position of four species of grebes among ten species of waterfowl, using three measures of community structure as axes: size (mean number of individuals), complexity (mean number of species), and predictability (mean Jaccard similarity coefficient). (Based on Figure 6 of Butterworth, 1982). WES = *Aechmophorus occidentalis*, HOR = *Podiceps auritus*, RED = *Podiceps grisegena*, EAR = *Podiceps nigricollis*, WID = *Anas americana*, RIN = *Aythya collaris*, BUF = *Bucephala albeola*, GAD = *Anas strepera*, MAL = *Anas platyrhynchos*, BWT = *Anas discors*, RUD = *Oxyura jamaicensis*, CAN = *Aythya valisineria*, SCA = *Aythya affinis*, WWS = *Melanitta fusca*. (Dashed line surrounds the grebes).


☆ Podicipedidae
○ Anatini
● Aythyini
■ Mergini
□ Oxyurini
PREDICTABILITY
.5
.3
.1
4
2
6
10
18
6
8
10
SIZE
2
6
10
14
18
COMPLEXITY
WID
RIN
BUF
GAD
MAL
WES
HOR
BWT
RED
EAR
RUD
CAN
SCA
WWS

contained significant proportions of species that were common, abundant and regularly co-occurred. Both the specificity of the parasites for grebes, and the food habits of the hosts that ensure transmission of those helminths, contribute to establishing and maintaining a core-satellite structure. The patterns of parasite distribution across hosts demonstrate that the parasite assemblages meet the necessary prerequisites for the formation of interactive communities.

F. Literature Cited

Baer, J.G. 1954. Revision taxonomique et etude biologique des cestodes de la famille des Tetrabothriidae, parasites d'oiseaux de haute mer et de mammiferes marine. Memoirs de l'Universite de Neuchatel Serie-in-Quarto 1:1-121.

Bush, A.O. 1980. Faunal similarity and infracommunity structure in the helminths of lesser scaup. Ph.D. thesis, Univ. of Alberta, Edmonton. 254 pp.

Bush, A.O., and J.C. Holmes. MS. Intestinal helminths of lesser scaup ducks: Patterns of association. Submitted to Can. J. Zool. 1985.

Butterworth, E.W. 1982. A study of the structure and organization of intestinal helminth communities in ten species of waterfowl (Anatinae). Ph.D. thesis, Univ. of Alberta, Edmonton. 217 pp.

Dubinina, M.N. 1964. Cestodes of the family Ligulidae and their taxonomy. pp. 173-186 In R. Ergens and B. Rysavy (eds.), Parasitic Worms and Aquatic Conditions. Proceedings of a Symposium held in Prague, Czchoslovakia, Oct. 29-Nov. 2, 1962. 265 pp.

Faaborg, J. 1976. Habitat selection and territorial behavior of the small grebes of North Dakota. Wilson Bull. 88:390-399.

Fager, E.W. 1957. Determination and analysis of recurrent groups. Ecology 38:586-595.

Fager, E.W., and A.R. Longhurst. 1968. Recurrent group analysis of species assemblages of demersal fish in the Gulf of Guinea. J. Fish. Res. Board Can. 25:1405-1421.

Fager, E.W., and J.A. McGowan. 1963. Zooplankton species groups in the North Pacific. Science 140:453-460.

Ferguson, R.S. 1981. Territorial attachment and mate fidelity by horned grebes. Wilson Bull. 93:560-561.

Fjeldsa, J. 1973. Distribution and geographical variation of the horned grebe, *Podiceps auritus*, (Linnaeus, 1758). Ornis Scand. 4:55-86.

Fjeldsa, J. 1983. Ecological character displacement and character release in grebes, Podicipedidae. Ibis 125:463-481.

Fox, D.J., and K.E. Guire. 1976. Documentation for MIDAS. Statistical Research Laboratory, Univ. of Michigan. 203 pp.

Gallimore, J.R. 1964. Taxonomy and ecology of helminths of grebes in Alberta. M.Sc. thesis, Univ. of Alberta, Edmonton. 167 pp.

Hair, J.D. 1975. The structure of the intestinal helminth communities of lesser scaup (*Aythya affinis*). Ph.D. thesis, Univ. of Alberta, Edmonton. 92 pp.

Hair, J.D., and J.C. Holmes. 1975. The usefulness of measures of diversity, niche width and niche overlap in the analysis of the helminth communities in waterfowl. Acta Parasit. Polon. 23:253-269.

Hanski, I. 1982. Dynamics of regional distribution: The core and satellite species hypothesis. Oikos 38:210-221.

Holmes, J.C. 1976. Host selection and its consequences. pp. 21-39 In C.R. Kennedy (ed.), Ecological Aspects of Parasitology. North-Holland Publ. Co., Amsterdam. 474 pp.

Holmes, J.C., R.D. Hobbs, and T.S. Leong. 1977. Populations in perspective: Community organization and the regulation of parasite populations. pp. 209-245. In Esch, G.W. (ed.), Regulation of Parasite Populations. Academic Press. New York.

Holmes, J.C., and P.W. Price. 1985. Communities of parasites. Chap. 9 In D.J. Anderson and J. Kikkawa (eds.), Community Ecology: Pattern and Process.

Blackwell Sci. Co., Oxford.

Price, P.W. 1984. Communities of specialists: Vacant niches in ecological and evolutionary time. pp. 510-523 In D.R. Strong, Jr., D. Simberloff, L.G. Abele and A.B. Thistle (eds.), Ecological Communities: Conceptual Issues and the Evidence. Princeton Univ. Press, Princeton N.J. 613 pp.

Rohde, K. 1978. Latitudinal differences in host specificity of marine Monogenea and Digenea. Mar. Biol. 47:125-134.

Root, R.B. 1967. The niche exploitation of the blue-green gnatcatcher. Ecol. Monogr. 37:317-350.

Rysavy, B., and K.M. Ryzhikov. 1978. Helminths of Fish-eating Birds of the Palearctic Region. I. Nematodes. Dr. W. Junk, Publ., The Hague. 318 pp.

Siegel, S. 1956. Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill, New York. 312 pp.

Sokal, R.R., and F.J. Rolfe. 1981. Biometry, The Principles and Practice of Statistics in Biological Research. Second Ed. W.H. Freeman and Co., San Francisco. 859 pp.

III. Functional Relationships and Microhabitat Distributions of Intestinal Helminths in Grebes: The Evidence for Interactive Communities

A. Abstract

In order to evaluate the significance of interaction as a structuring force, patterns of microhabitat distribution in infracommunities of four species of grebes (Podicipedidae), were examined. Core and recurrent group species (those parasites that were common and frequently co-occurred), resided in predictable locations along the length of the small intestine. Total occupied ranges, a measure of fundamental niche, were wide and variation in position of helminths in different species of hosts suggested a broad tolerance for conditions along the intestine. Actual positions in each infracommunity (a measure of realized niche) were significantly smaller than fundamental niches.

Complementarity in distributions of congeneric species and reductions in overlap between species were interpreted as evidence for interspecific interaction. In addition, a large cestode in *Podiceps grisegena*, *Dioecocestus asper*, had significant effects on the distributions and numbers of other helminths. Destruction of the intestinal mucosa, likely caused by pressure necrosis, was considered the mechanism of interference.

Although interactions between species were considered important in organizing the structure of the infracommunities, two features suggestive of isolationist communities were also noted. The communities in grebes were not saturated. Analysis of the distributions of members of three guilds in each host species, revealed vacant niches. In addition, core species were not more evenly spread in niche space than would be expected through random placement. A model of habitat selection, mediated by differential selection pressures in three parts of the intestine, was proposed. The model predicts the presence of isolationist species in the relatively unfavorable proximal and distal ends of the intestine, and interactive species in the favorable mid-intestine.

B. Introduction

Many parasites are known to occupy precise, predictable and limited locations within their hosts (see reviews in Crompton, 1973; Holmes, 1973; Crompton and Nesheim, 1975). Price (1980, 1984) argued that the generality of this observation was the consequence of highly specialized organisms exploiting complex environments with steep gradients in environmental conditions or resources. A group of such species, each adapted independently to a restricted location in a host, would form an isolationist community.

An alternative explanation for the site specificity demonstrated by parasites was limitation of microhabitat distribution mediated by interspecific interactions (Holmes, 1973). A group of species whose distributions were limited in this way would form an interactive community. Holmes and Price (1985) contrasted these two types of communities and presented several attributes that could be used to differentiate isolationist from interactive assemblages.

The basic difference between these views of communities obviously centers on whether the realized distributions of the component species are limited primarily by the degree of specialization or by the presence of other species. The degree of specialization of intestinal parasites can be considered to be the inverse of their physiological tolerance to the range of conditions present in different regions of the intestine. This range of tolerance is analogous to Hutchinson's (1957) concept of fundamental niche. The best measure of a helminth's fundamental niche would be its potential distribution in controlled monospecific infections; in the absence of such data, the fundamental niche may be estimated by the distribution of the species summed across all infracommunities in which it occurred (Bush, 1980; Butterworth, 1982). Realized niches, the ranges actually occupied in individual infracommunities, are subsets of the fundamental niches. Presumably, realized niches represent the optimal part of the fundamental niche (where infrapopulations are small) or the portions of the fundamental niches actually available to species subjected to interactions with other helminths (Pianka, 1975).

Because isolationist communities are assumed to be unsaturated aggregations of specialists, fundamental niches should be small and similar in size to realized niches, and vacant niches in infracommunities should be common. Niche breadths may increase with increasing populations, but there should be little or no evidence of interactions (such as displacement); overlaps between species should increase with increases in combined population size. Finally, species should be distributed along the intestine either at random, or according to the quality of the habitat.

Conversely, interactive communities should include species that are more generalized in microhabitat use. Fundamental niches should be relatively broad, and realized niches should be reduced in the presence of other guild members. Interactive communities are assumed to be saturated and to have few vacant niches. Niches should be sensitive to variations in population size but overlaps with other species should be avoided. The core species should be distributed more evenly along the intestine than expected by chance (Hanski, 1982) and congeners should be complementary in their use of the habitat (Brown, 1975; Pianka, 1975).

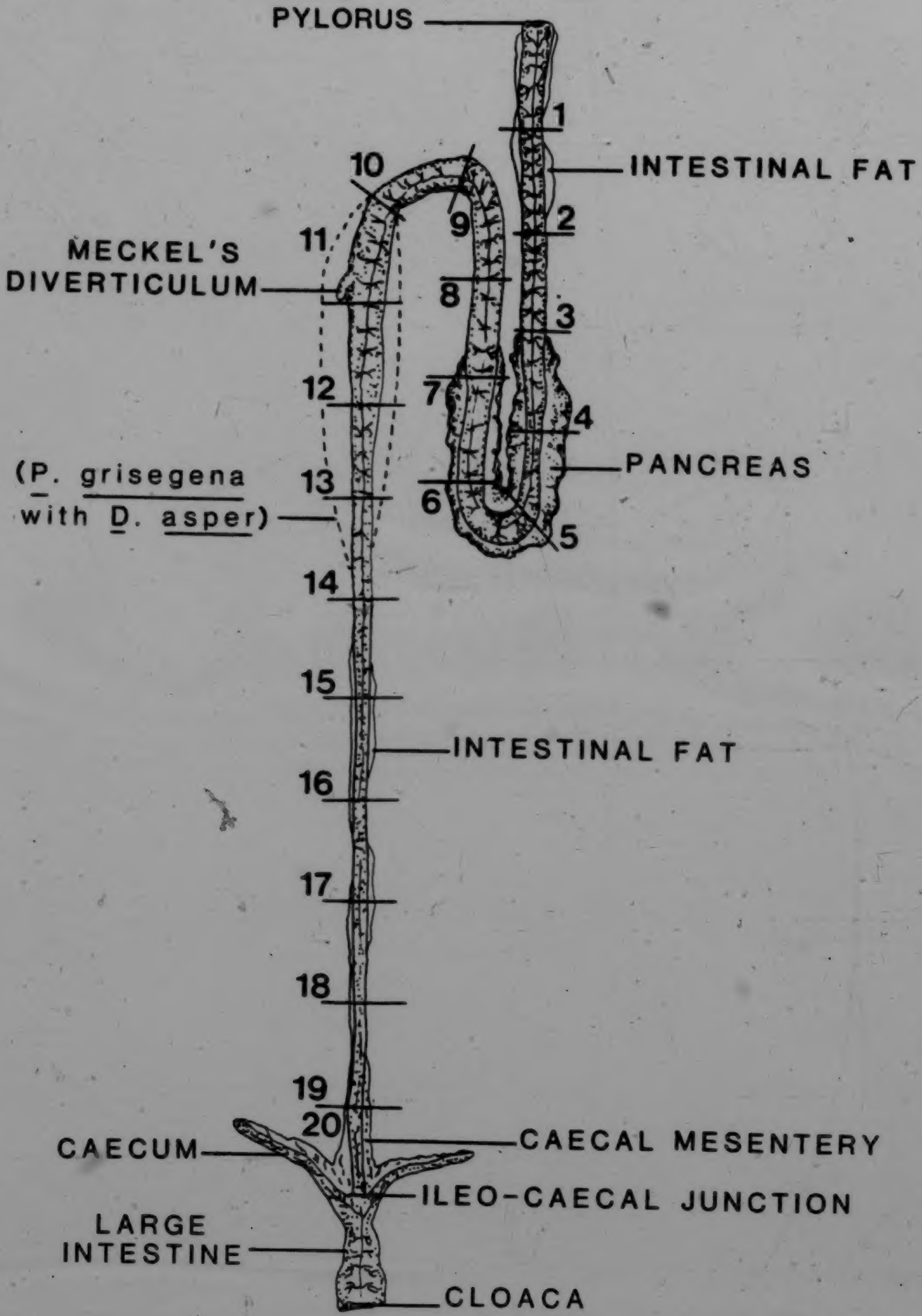
In the second chapter, I showed that three of four grebe species had communities of helminths with high proportions of co-occurring, core species. These were present in reasonably high populations and conferred a high degree of predictability to the communities. In this chapter, I will examine the functional relationships and the patterns of microhabitat distributions of core species, in order to evaluate the importance of interaction and specialization as forces responsible for maintaining intestinal helminth community structure in grebes.

C. Materials and Methods

Birds were collected during the breeding season (May to September) on nine lakes in Alberta by shooting. Birds were weighed, intestinal tracts were removed and quick frozen. Later in the laboratory, intestines were partially thawed and the length of each was measured. The small intestine was divided into 20 equal sections, each of which was placed in a separate vial and maintained frozen until each was examined individually later. The large intestine and caeca were also stored and examined separately. See Chapter 2 for details of these procedures. The relation of sections to intestinal features is depicted in Figure 1.

The locations of the median, anterior-most and posterior-most individuals of each species of helminth in each small intestine were determined and expressed as percentages of the length of the small intestine. The pyloric sphincter-duodenal junction was assigned a value of 0%, the ileo-caecal junction a value of 100%. Within a section, individuals were assumed to be equally spaced, with the space between the end of the segment and the first (or last) individual assumed to be one-half of the distance between individuals. Distance measures were calculated by a

Figure 1. Relationship of 20 equal sections to morphological features of the intestine of a grebe.


PYLORUS
INTESTINAL FAT
MECKEL'S DIVERTICULUM
PANCREAS
(P. grisegena with D. asper)
INTESTINAL FAT
CAECUM
CAECAL MESENTERY
ILEO-CAECAL JUNCTION
LARGE INTESTINE
CLOACA

FORTRAN program written by Drs. J.F. Addicott and J.C. Holmes. For tapeworms, unless indicated otherwise, the position of the scolex was considered to represent the position of the individual. Overlaps were calculated using percent similarity (equation 1 of Hurlbert, 1978) by an APL program written by Mr. N. Weimer.

The intestines of three *Podiceps grisegena* were prepared for histological examination. Intestines were removed, measured and divided in 20 equal parts, each of which was fixed and preserved in individual vials of Bouin's fixative, and post-fixed in 10% neutral buffered formalin. A sample from the middle of each segment was serially sectioned transversely, at 7 um, and stained in eosin-haematoxylin. For each segment, three individual intestinal sections were chosen, using a random number table, for measurement. The maximum outside diameter, and the widths of the mucosa, sub-mucosa and muscularis were measured and the number of villi counted. Mean values of the measurements for the three specific histological sections were considered representative of that intestinal segment.

D. Results

General Patterns of Distribution

The sizes of the intestines of grebes varied among species (Table 1). There was almost a threefold difference

Table 1. Selected morphological characteristics of four species of grebes.

	Aechmophorus occidentalis (*n* = 20)	*Podiceps grisegena* (*n* = 33)	*Podiceps nigricollis* (*n* = 31)	*Podiceps auritus* (*n* = 7)
Body Weight gms (SD)	1262(247)	1124(159)	366(49)	393(43)
C.V.[1] %	20	14	13	11
Intestine Length cms (SD)	139.2(19.7)	118.4(14.9)	104.1(14.0)	99.4(4.3)
C.V. %	14	13	4	4
Range in Intestine Length cms	108-205	88-150	72-138	94-107
Mean Section with Meckel's Diverticulum (SD)	11.4(0.5)	11.2(0.9)	10.7(0.5)	10.7(1.0)
C.V. %	4	8	5	9

---

[1] Coefficient of variation, 100 X SD/Mean

in intestinal length between the smallest *Podiceps nigricollis* and the largest *Aechmophorus occidentalis*. Mean lengths ranged from 139 cm for *A. occidentalis* to 99 cm for *Podiceps auritus*. Coefficients of variation of intestinal length were greater for the two large grebes (*A. occidentalis* and *Podiceps grisegena*) than for the two small grebes (*P. nigricollis* and *P. auritus*). That this greater variation is not due to differential contraction in the more muscular fore-guts of large grebes is indicated by the more posterior location of a mid-intestinal marker, Meckel's diverticulum, in these birds. Similar coefficients of variation in position of this feature in large and small grebes also suggest that differential contraction is not important. The greater variation in intestinal length may to be due to the greater variation in body size in the large grebes (Table 1). Despite the differences in intestinal size, the relative positions of characteristics such as the pancreas, its ducts, and Meckel's diverticulum were similar (Fig. 1, Table 1). Therefore, locations expressed as a percent of small intestine length are comparable among grebes.

Parasites can potentially inhabit all 20 sections of the small intestine in all grebes; no sections were always unoccupied. Large grebes had higher proportions of unoccupied sections than small grebes, with a maximum of 13% in *A. occidentalis* (Table 2). The distribution of vacant sections was not random, but increased toward the

Table 2. Overall distributions of intestinal helminths in four species of grebes, Podicipedidae.

	Aechmophorus occidentalis (*n*=20)	*Podiceps grisegena* (*n*=33)	*Podiceps nigricollis* (*n*=31)	*Podiceps auritus* (*n*=7)
No. Species/Section				
range	0-5	0-7	0-9	0-5
overall mean	2.0	2.9	2.6	2.0
range, means/section	0.6-2.5	1.0-4.5	1.0-3.9	0.7-2.7
C.V.[1]	.33-1.7	.26-.96	.28-.83	.33-1.04
No. Worms/Section				
range	0-261	0-1722	0-4886	0-1781
overall mean	25	132	292	173
range, means/section	2-55	5-362	75-534	17-374
C.V.	.70-2.48	.99-2.[illegible]9	.68-3.66	1.17-2.10
Percent of Sections Unoccupied	13	11	4	5

---

[1] Coefficient of Variation, SD/Mean

ileo-caecal junction. For all grebes, the last intestinal section was the most frequently unoccupied (Fig. 2).

All four grebe species were characterized by a reduction in the mean number of species of helminths per section (species richness) towards the posterior end of the intestine (Fig. 3). Maximum species richness for *P. nigricollis* occurred in the mid intestine and for *P. grisegena* in the anterior quarter. For *A. occidentalis* there was little change over the anterior 3/4 of the intestine, and the pattern in *P. auritus* was bimodal with peaks in the duodenal region and at 75% of the length of the intestine. *A. occidentalis* and *P. auritus* tended to have fewer species per section throughout the intestine than *P. grisegena* and *P. nigricollis*. Coefficients of variation for all grebes increased from anterior to posterior, indicating that the latter region was the least predictable with regards to species richness.

Three grebes, *A. occidentalis*, *P. grisegena*, and *P. auritus*, had the same pattern of habitat use by parasites as measured by mean number of worms per section (Fig. 4). Maximal values occurred in the duodenal region followed by a gradual decline toward the posterior end. In *P. nigricollis*, secondary peaks in the mid and posterior intestine were superimposed on this pattern. As in the case of species richness, coefficients of variation increased from the anterior to the posterior part of the intestine; they were especially high in the posterior sections in *P. nigricollis*.

Figure 2. Distribution of intestinal sections without parasites in four species of grebes.

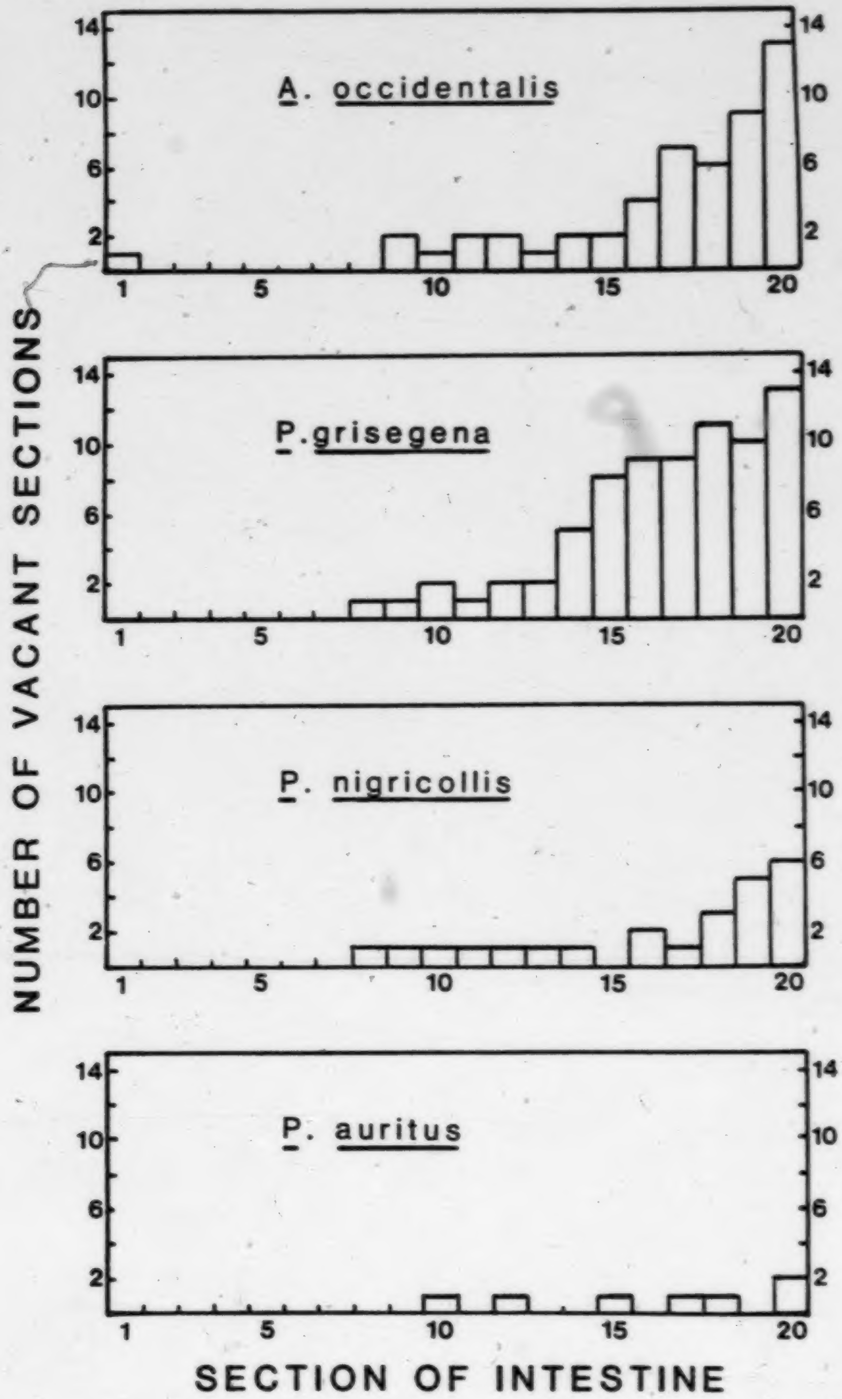

NUMBER OF VACANT SECTIONS
A. occidentalis
P. grisegena
P. nigricollis
P. auritus
14
10
6
2
1
5
10
15
20
SECTION OF INTESTINE

Figure 3. Mean number of helminth species per section of intestine (with coefficient of variation), in four species of grebes.

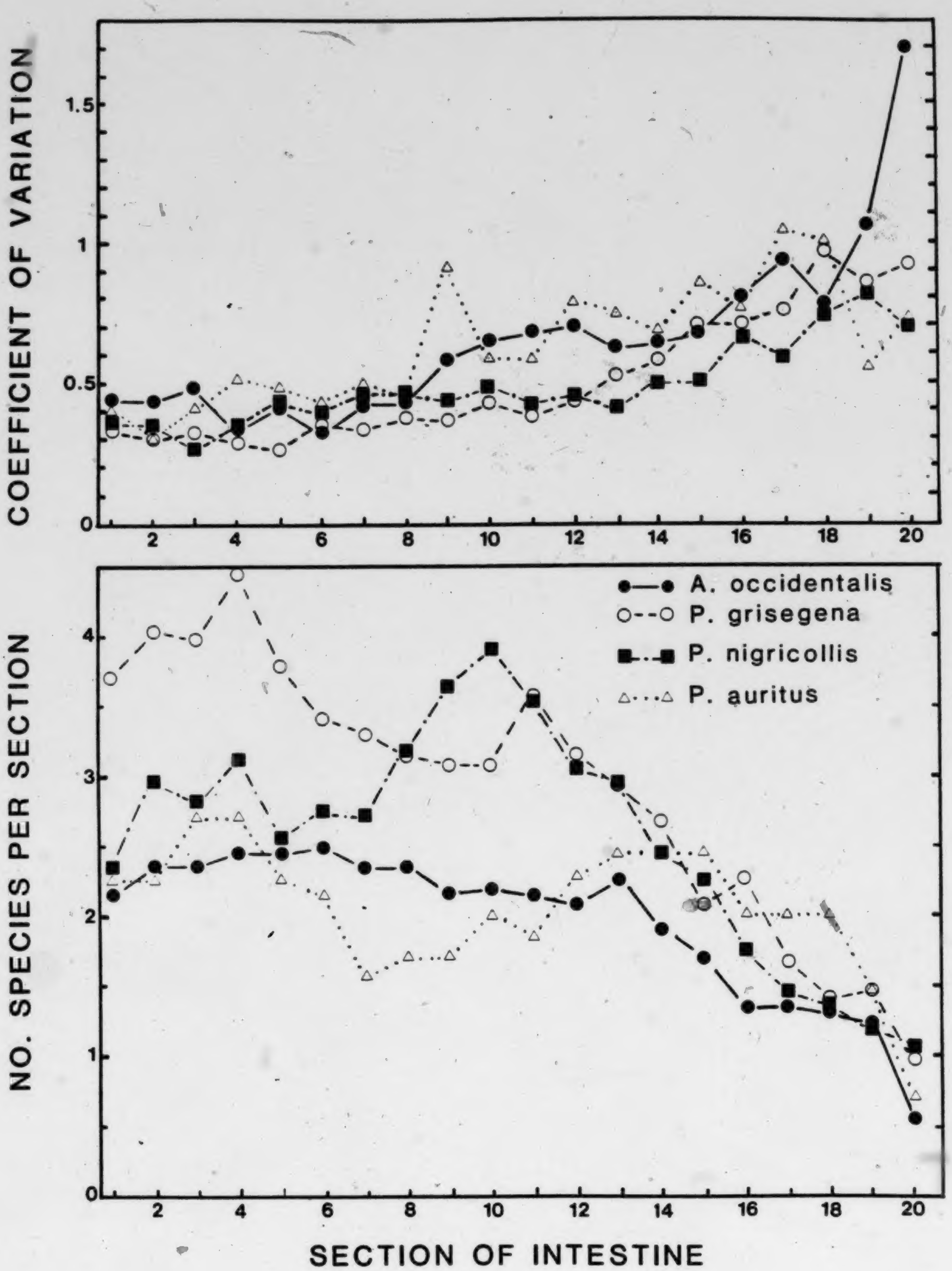
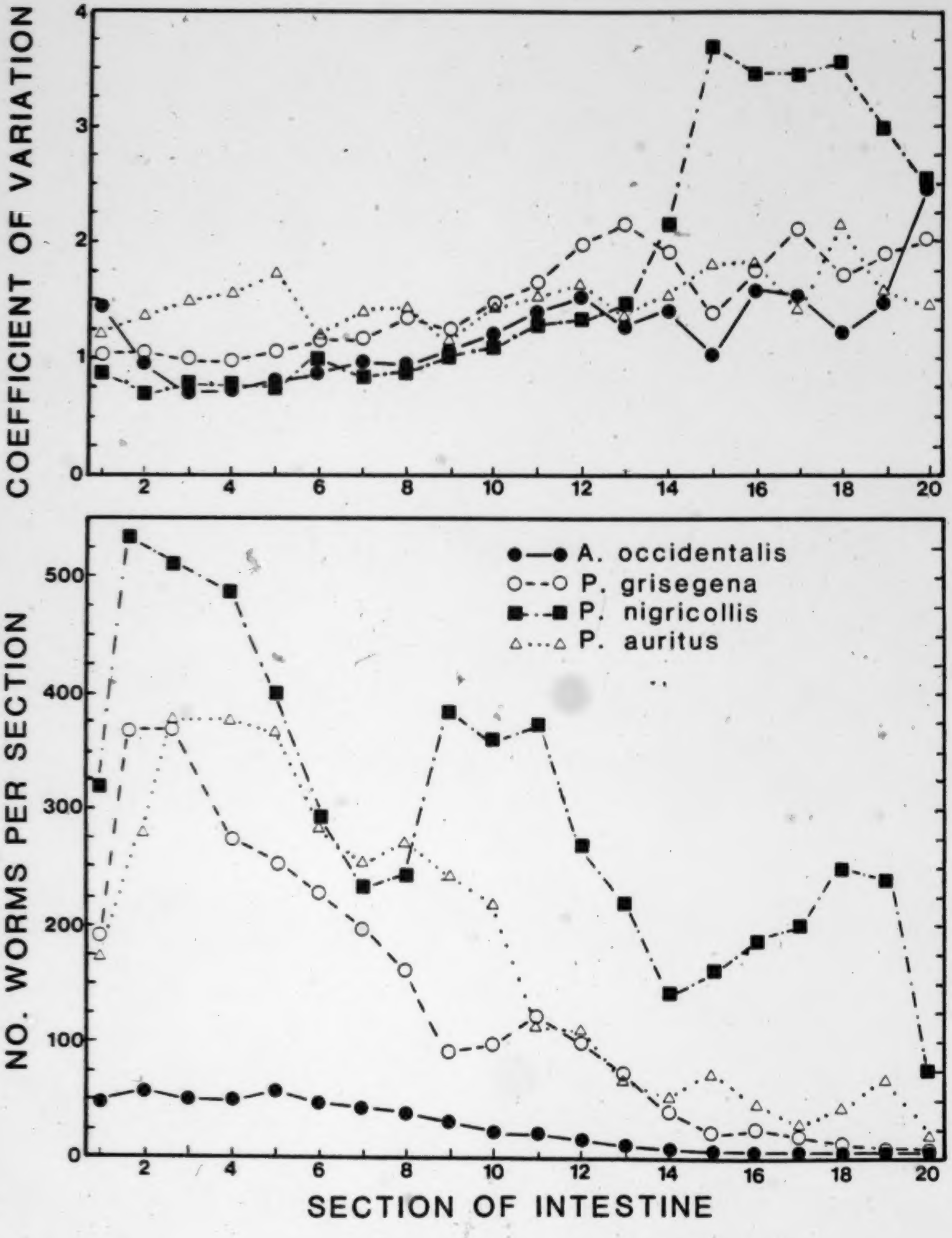

COEFFICIENT OF VARIATION
0
0.5
1
1.5
2
4
6
8
10
12
14
16
18
20
NO. SPECIES PER SECTION
0
1
2
3
4
A. occidentalis
P. grisegena
P. nigricollis
P. auritus
SECTION OF INTESTINE

Figure 4. Mean number of individual helminths per intestinal section (with coefficient of variation), in four species of grebes.


COEFFICIENT OF VARIATION
0
1
2
3
4
2
4
6
8
10
12
14
16
18
20
NO. WORMS PER SECTION
0
100
200
300
400
500
●—● A. occidentalis
○--○ P. grisegena
■-·-■ P. nigricollis
△····△ P. auritus
2
4
6
8
10
12
14
16
18
20
SECTION OF INTESTINE

The posterior part of the intestine was the least predictable in terms of the numbers of both species and worms per section.

One measure of the location of a species of helminth is the position of its medianth individual in each host. The mean of these positions is a measure of the usual location of that species (Tables 3 to 6). Frequency distributions of mean medians in each host species show that the species of helminths were not concentrated in (nor absent from) any particular part of the intestine (Fig. 5). Chi square tests indicated that the numbers of species in each quarter of the intestine did not differ from uniform distributions (*P. nigricollis*, X^2 (3 d.f.)= 6.37, $.10>P>.05$; other grebes X^2= 1.1, $P>.5$). Therefore, the patterns in species richness and numbers of worms described above are not due to differences in the numbers of species adapted to live in different portions of the intestine.

Bush and Holmes (1983) proposed a method using MacArthur's (1957) broken-stick model to test the distribution of species in individual infracommunities. This test provides a quantitative technique for determining if the positions of species distributed along a gradient are clumped, randomly distributed, or more evenly distributed than would be expected by chance alone. The null hypothesis of independent, random distribution could not be rejected for data from infracommunities in *A. occidentalis* (12 infracommunities above, 8 below predicted values), *P.*

Table 3. Locations of intestinal helminths in 20 *Aechmophorus occidentalis* from Alberta, Canada. Locations are expressed as percents of intestinal length. 0 = pylorus, 100 = ileo-caecal junction.

Helminth	Prevalence	Mean Intensity	Mean Median (SD)	Mean Anterior (SD)	Mean Posterior (SD)	Mean Range[1] (SD)	Total Occupied Range
Pararetinometra lateralacantha	1/20	2	2.5	1.3	3.8	2.5	3
Contracaecum ovale	1/20	1	7.5	7.5	7.5	-	-
*Tylodelphys podicipina**	15/20	67	17.3(9.6)	3.0(5.7)	50.4(19.8)	50.8(18.4)	79
Tatria biremis	7/20	5	17.9(11.6)	8.3(4.5)	21.8(14.8)	23.7(14.7)	42
*Dubininolepis furcifera**	18/20	332	19.7(6.5)	0.9(1.8)	60.4(19.7)	59.5(19.8)	97
Diorchis sp. P.	2/20	2	30.0(24.8)	29.4(25.6)	30.6(23.9)	2.5(0)	36
*Petasiger nitidus**	17/20	115	36.7(18.2)	11.7(16.7)	67.5(23.1)	59.4(20.5)	100
Apatemon gracilis	5/20	47	44.2(29.4)	19.9(27.8)	68.4(40.2)	60.7(32.5)	99
Tatria decacantha	1/20	3	52.5	47.5	57.5	10	10
*Wardium paraporale**	20/20	25	54.4(19.7)	35.5(17.6)	74.7(23.2)	41.3(17.2)	92
Dubininolepis podicipina	1/20	10	56.7	47.5	62.5	15	15
*Ligula intestinalis**	16/20	8	70.6(9.6)	61.8(10.4)	80.0(10.6)	19.3(11.1)	47
Capillaria obsignata[2]	2/20	3	80.0(17.7)	67.5(17.7)	92.5(17.7)	-	25
Polymorphus marilis	2/20	2	85.0(3.5)	84.4(2.7)	85.6(4.4)	2.5	6
Tetrabothrius immerinus	8/20	3	88.5(6.5)	78.9(21.7)	90.5(6.7)	23.2(21.9)	66
Schistocephalus solidus	6/20	6	91.1(3.6)	88.1(5.7)	94.2(3.5)	9.1(3.5)	18

---

[1] Range can differ from simple (mean posterior - mean anterior) calculation if infections with a single individual occurred, thus providing no range measurement for that infection.

[2] Most of these occurred in the caeca. Locations are for those in the small intestine only.

* Core species (see text).

Table 4. Locations of intestinal helminths in 33 Podicpes grisegena from Alberta, Canada. Locations are expressed as percents of intestinal length. 0 = pylorus, 100 = ileo-caecal junction.

Helminth	Prevalence	Mean Intensity	Mean Median (SD)	Mean Anterior (SD)	Mean Posterior (SD)	Mean Range[1] (SD)	Total Occupied Range
Pararetinometra lateralacantha	6/33	56	2.8(0.5)	0.2(0.3)	8.0(3.1)	7.8(3.3)	12
Tylodelphys podicipina*	30/33	179	9.3(5.8)	1.2(3.4)	30.2(18.1)	30.0(18.4)	79
Dubininolepis furcifera*	32/33	109	9.4(3.5)	1.4(2.4)	20.2(8.8)	18.0(8.6)	44
Tatria biremis*	28/33	377	9.7(4.0)	1.3(2.0)	23.8(11.2)	22.5(12.2)	47
Diorchis sp. O	1/33	3	13.8	11.3	17.5	6.3	6
Cotylurus sp.	1/33	1	22.5	22.5	22.5	-	-
Schistotaenia srivastavai*	24/33	18	22.7(5.2)	19.4(6.2)	27.5(6.9)	9.7(8.9)	33
Retinometra sp.	1/33	1	27.5	27.5	27.5	-	-
Petasiger nitidus*	31/33	1025	28.9(6.6)	5.5(10.8)	76.8(19.5)	71.3(28.7)	100
Tatria decacantha*	27/33	1085	36.2(15.5)	13.5(16.4)	67.8(15.3)	54.3(25.4)	94
Schistotaenia tenuicirrus	1/33	1	37.5	37.5	37.5	-	-
Wardium paraporale*	32/33	113	40.9(19.5)	25.4(14.0)	63.8(21.6)	38.4(21.5)	94
Apatemon gracilis	5/33	2	49.5(28.8)	38.3(18.3)	51.8(29.2)	16.9(16.0)	80
Contracaecum ovale*	26/33	21	54.3(8.6)	43.8(12.2)	66.9(13.4)	25.0(20.0)	91
Dioecocestus asper*	24/33	2	54.4(17.0)	45.4(19.4)	57.5(16.2)	13.2(10.5)	76
Tetrabothrius immerinus	4/33	7	58.7(42.9)	44.2(31.8)	63.1(45.1)	18.9(16.2)	92
immature strigeids	7/33	4	62.7(33.0)	60.5(33.9)	76.6(27.4)	28.3(37.3)	83
Ligula intestinalis	10/33	28	67.2(26.5)	57.6(28.0)	73.9(29.5)	19.2(21.2)	95
Capillaria obsignata*[2]	29/33	21	70.9(25.1)	43.4(31.0)	79.8(27.5)	46.3(34.4)	97
Schistocephalus solidus	13/33	49	82.7(14.4)	62.4(22.1)	91.9(11.2)	32.0(21.3)	84
Corynosoma constrictum	4/33	2	88.4(6.6)	84.7(9.0)	92.5(0)	15.6(0.9)	16
Polymorphus marilis	1/33	6	90.0	85.8	94.2	8.3	8

---

[1] Range can differ from simple (mean posterior - mean anterior) calculation if infections with a single individual occurred, thus providing no range measurement for that infection.

[2] Most of these occurred in the caeca. Locations are for those in the small intestine only.

* Core species (see text).

Table 5. Locations of intestinal helminths in 31 *Podiceps nigricollis* from Alberta, Canada.
Locations are expressed as percents of intestinal lengths. 0 = pylorus, 100 = ileo-caecal junction.

Helminth	Prevalence	Mean Intensity	Mean Median (SD)	Mean Anterior (SD)	Mean Posterior (SD)	Mean Range[1] (SD)	Total Occupied Range
Pararetinometra lateralacntha	4/31	11	5.1(2.4)	3.0(3.9)	7.9(0.7)	7.4(0.2)	9
Tylodelphys podicipina	2/31	2	7.5	7.5	7.5	-	-
Trichobilharzia sp.	1/31	1	12.5	12.5	12.5	-	-
Nadejdolepis sp.	15/31	883	12.7(3.5)	4.6(3.6)	21.6(11.0)	19.4(12.9)	47
Dubininolepis furcifera	7/31	61	12.8(6.0)	4.1(3.6)	24.2(10.1)	20.1(8.7)	42
Diorchis sp. O*	26/31	220	14.0(9.6)	3.5(4.9)	27.6(16.0)	26.1(14.9)	99
Schistotaenia srivastavai	2/31	2	15.0(3.5)	14.4(4.4)	15.6(2.7)	2.5	6
*Tatria biremis**	31/31	2794	18.1(6.5)	0.1(0.5)	51.5(15.0)	51.4(15.1)	97
Petasiger nitidus	5/31	44	20.0(7.1)	8.7(11.9)	35.7(19.0)	27.0(22.0)	67
Schistotaenia colymba	16/31	7	20.9(3.2)	18.0(4.7)	23.1(3.9)	8.1(5.6)	22
Apatemon gracilis	9/31	15	40.4(18.1)	19.7(20.2)	62.1(29.7)	63.5(25.5)	90
Microsomacanthus sp. T	5/31	58	43.2(31.8)	27.8(17.2)	57.4(24.8)	29.6(17.8)	92
*Dubininolepis podicipina**	29/31	65	43.8(10.9)	30.3(14.0)	61.8(14.9)	31.5(17.5)	92
Schistocephalus solidus	3/31	2	47.1(8.9)	45.4(7.5)	49.2(10.4)	5.6(0.9)	20
Contracaecum ovale	11/31	4	47.5(20.5)	38.5(24.5)	55.5(22.7)	27.4(25.3)	81
Diorchis sp. P*	26/31	1635	51.2(4.5)	34.0(7.7)	77.2(10.9)	43.2(15.0)	82
Tatria decacantha	26/31	53	52.6(7.5)	45.5(7.0)	67.0(13.9)	21.7(12.8)	62
Lateriporus skrjabini	4/31	295	52.8(20.2)	47.8(23.4)	63.2(16.3)	20.6(7.9)	51
Echinatrium sp. Y	2/31	19	55.1(3.6)	48.9(2.0)	75.6(11.5)	26.7(9.5)	36
Ligula intestinalis	1/31	4	60.0	37.5	72.5	35.0	35
Microsomacanthus sp. W	1/31	12	62.5	56.3	83.8	27.5	28
Parafimbriaria websteri	2/31	3	70.0(3.5)	66.9(8.0)	73.1(0.9)	12.5	13
Capillaria obsignata[2]	12/31	5	72.2(25.7)	61.7(29.7)	77.0(27.3)	27.5(25.3)	91
*Wardium paraporale**	31/31	1183	74.4(13.7)	50.4(13.1)	94.7(8.2)	43.9(13.6)	70
Polymorphus marilis	1/31	10	81.0	66.3	87.5	21.5	22
Microsomacanthus sp. Z	3/31	19	92.7(3.3)	83.4(8.4)	97.6(2.7)	14.1(10.0)	28

[1] Range can differ from simple (mean posterior - mean anterior) calculation if infections with a single individual occurred, thus providing no range measurement for that infection.

[2] Most of these occurred in the caeca. Locations are for those in the small intestine only.

* Core species (see text).

Table 6. Locations of intestinal helminths in seven *Podiceps auritus* from Alberta, Canada. Locations are expressed as percents of intestinal lengths. 0 = pylorus, 100 = ileo-caecal junction.

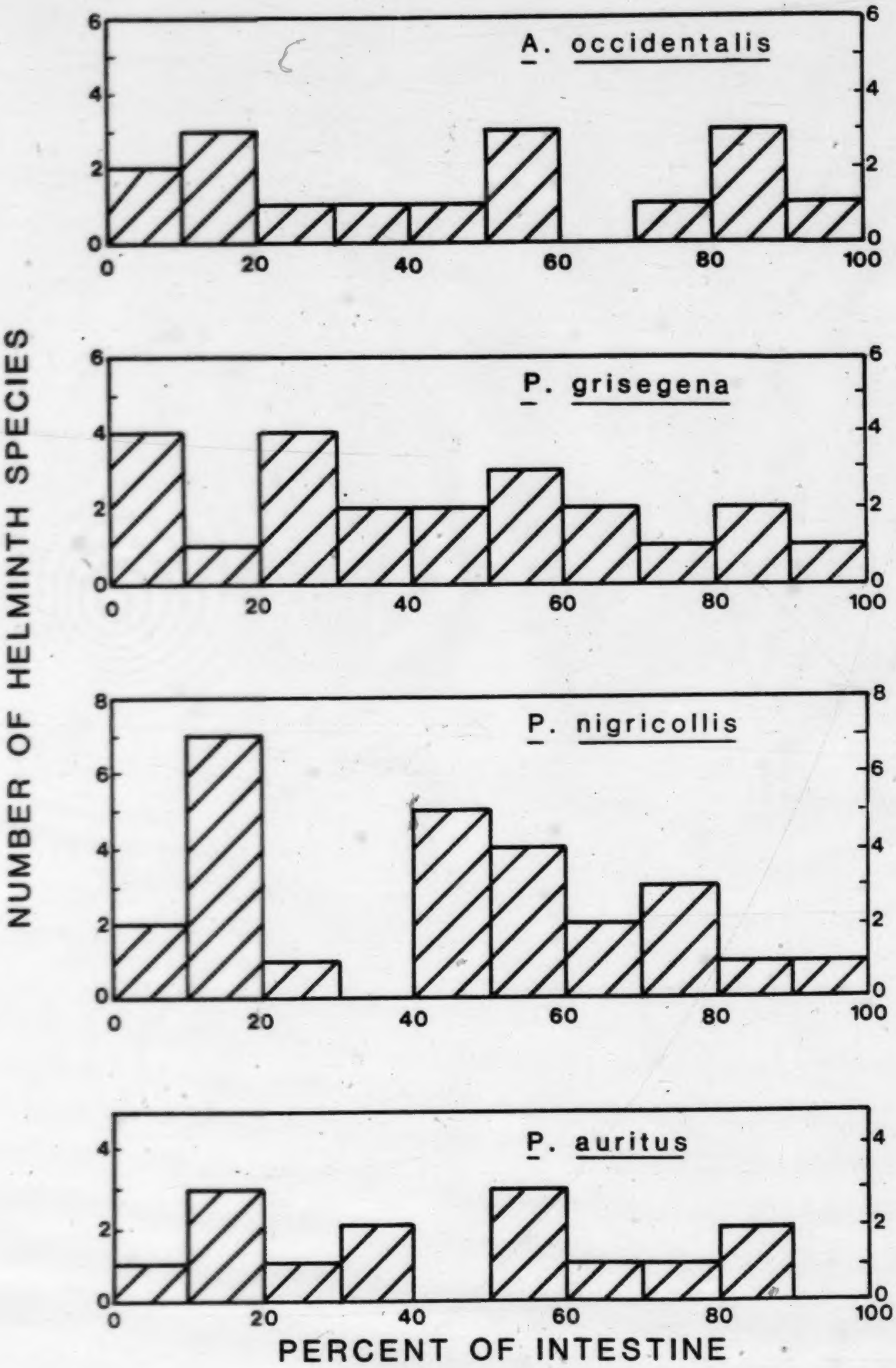
Helminth	Prevalence	Mean Intensity	Mean Median (SD)	Mean Anterior (SD)	Mean Posterior (SD)	Mean Range[1] (SD)	Total Occupied Range
Diorchis sp. O**	3/7	6	6.1(2.0)	3.9(5.1)	10.8(4.7)	13.9	14
*Dubininolepis furcifera***	4/7	32	14.0(16.3)	0.4(0.5)	32.9(37.8)	32.5(38.0)	99
Schistotaenia colymba	1/7	2	15.0	12.5	17.5	5.0	5
*Schistotaenia srivastavai***	3/7	6	17.0(1.1)	13.2(3.0)	23.0(5.2)	13.1(3.3)	17
*Tatria biremis**	7/7	1616	26.2(12.2)	0.4(0.9)	61.4(21.2)	61.0(21.1)	89
*Petasiger nitidus***	3/7	131	32.2(20.1)	1.5(1.0)	69.5(35.1)	68.0(36.0)	94
Dubininolepis podicipina	1/7	5	38.8	32.5	43.8	11.3	11
Tatria decacantha	2/7	13	50.1(23.9)	45.5(21.5)	63.5(34.3)	17.9(12.8)	67
Diorchis sp. P	1/7	23	53.6	43.6	70.0	26.5	26
Ligula intestinalis	1/7	1	57.5	57.5	57.5	-	-
*Contracaecum ovale***	4/7	4	62.6(18.4)	46.3(27.8)	66.8(20.0)	27.4(25.9)	65
*Wardium paraporale**	7/7	210	77.9(19.1)	45.3(23.1)	97.7(3.3)	52.4(23.1)	82
Tetrabothrius immerinus	3/7	2	83.8(8.8)	81.7(9.0)	91.3(2.2)	9.6(10.2)	21
Apatemon gracilis	1/7	1	87.5	87.5	87.5	-	-

[1] Range can differ from simple (mean posterior - mean anterior) calculation if infections with a single individual occurred, thus providing no range measurement for that infection.

* Core species (see text).

** Secondary species (see text).

Figure 5. Frequency distributions of intestinal helminth species, based on mean median positions, in four species of grebes.


A. occidentalis
P. grisegena
P. nigricollis
P. auritus
NUMBER OF HELMINTH SPECIES
PERCENT OF INTESTINE
0
2
4
6
8
20
40
60
80
100

auritus (3 above, 4 below) and *P. nigricollis* (14 above, 17 below). However, data from infracommunities in *P. grisegena* (25 above, 8 below predicted values; Z= 3.13, P< .05) indicated a clumped distribution. The distance between the position of the posterior-most species and the posterior end of the intestine was the largest segment in 14 of 33 (42%) of the *P. grisegena* infracommunities. This suggests that the broken-stick model may not be appropriate in this instance.

Specific Distributions

Locations of core (and secondary) and recurrent group (and associate) species in each host are presented in Fig. 6. Note that in each grebe, these helminth species are spread, although not too evenly, throughout the intestine.

To determine if the order of occurrence of these helminths in each host is predictable, all helminth species were ranked, by order of position in each host, and Spearman rank correlations were calculated for all pairs of infracommunities sharing five or more helminth species. Although rho can vary from -1 (a negative correlation) to +1, the 936 comparisons were concentrated near +1 (Fig. 7). Mean values of rho ranged from a low of 0.714 for *A. occidentalis*, to 0.850 for *P. auritus* (Table 7). The order of occurrence of core and recurrent group helminths along the intestinal tracts in each host species was highly predictable.

Figure 6. Distributions of core, secondary, recurrent group and associate species in the intestines of four grebes. A = *Aechmophorus occidentalis*, B = *Podiceps grisegena*, C = *Podiceps nigricollis*, D = *Podiceps auritus*.

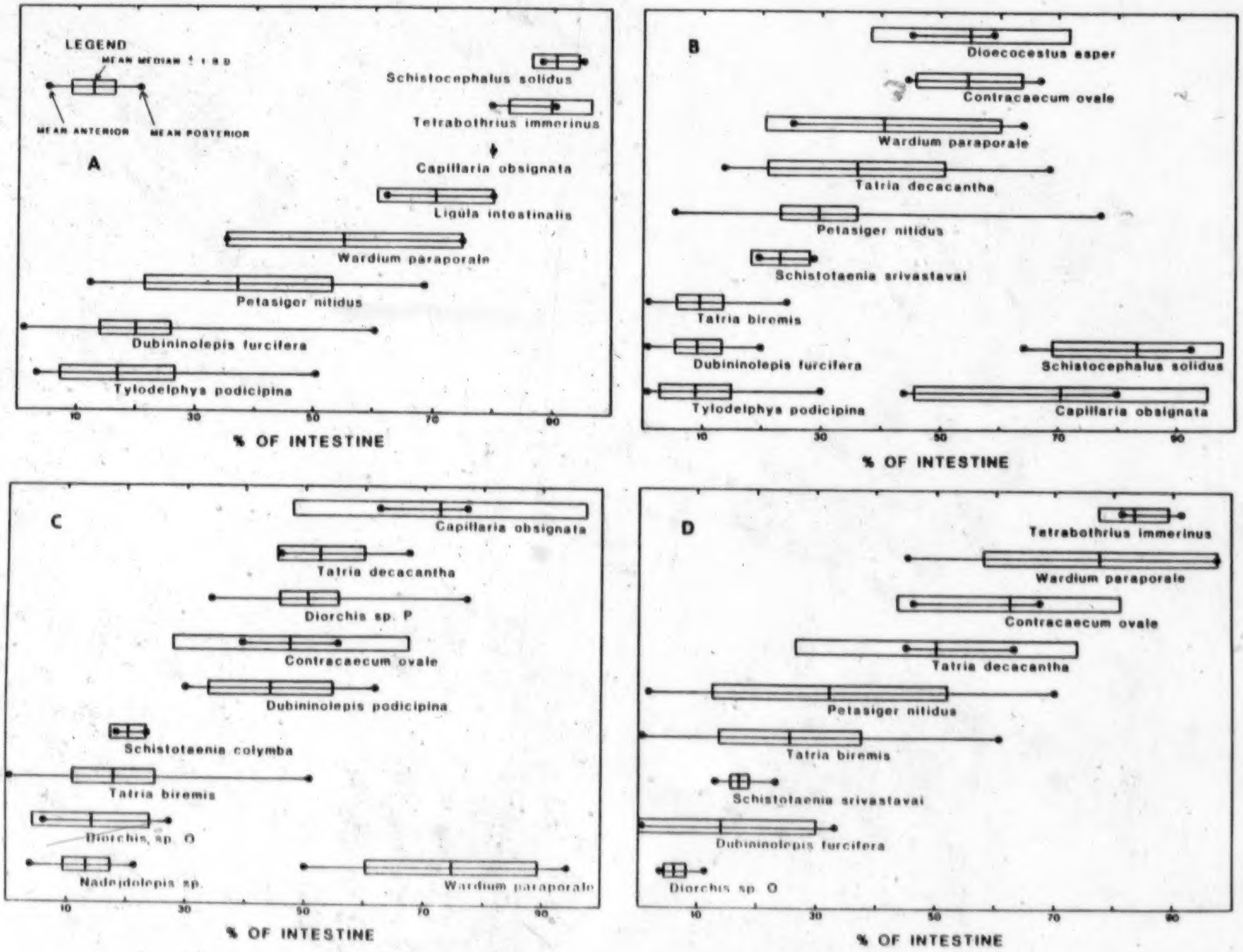

A
LEGEND
MEAN MEDIAN ± 1 S.D.
MEAN ANTERIOR
MEAN POSTERIOR
Schistocephalus solidus
Tetrabothrius immerinus
Capillaria obsignata
Ligula intestinalis
Wardium paraporale
Petasiger nitidus
Dubininolepis furcifera
Tylodelphys podicipina
10
30
50
70
90
% OF INTESTINE
B
Dioecocestus asper
Contracaecum ovale
Wardium paraporale
Tatria decacantha
Petasiger nitidus
Schistotaenia srivastavai
Tatria biremis
Dubininolepis furcifera
Schistocephalus solidus
Tylodelphys podicipina
Capillaria obsignata
10
30
50
70
90
% OF INTESTINE
C
Capillaria obsignata
Tatria decacantha
Diorchis sp. P
Contracaecum ovale
Dubininolepis podicipina
Schistotaenia colymba
Tatria biremis
Diorchis sp. O
Nadejdolepis sp.
Wardium paraporale
10
30
50
70
90
% OF INTESTINE
D
Tetrabothrius immerinus
Wardium paraporale
Contracaecum ovale
Tatria decacantha
Petasiger nitidus
Tatria biremis
Schistotaenia srivastavai
Dubininolepis furcifera
Diorchis sp. O
10
30
50
70
90
% OF INTESTINE

Figure 7. Frequency distribution of Spearman rank correlation rho values for all pairs of infracommunities that shared five or more helminth species, for each species of grebe.

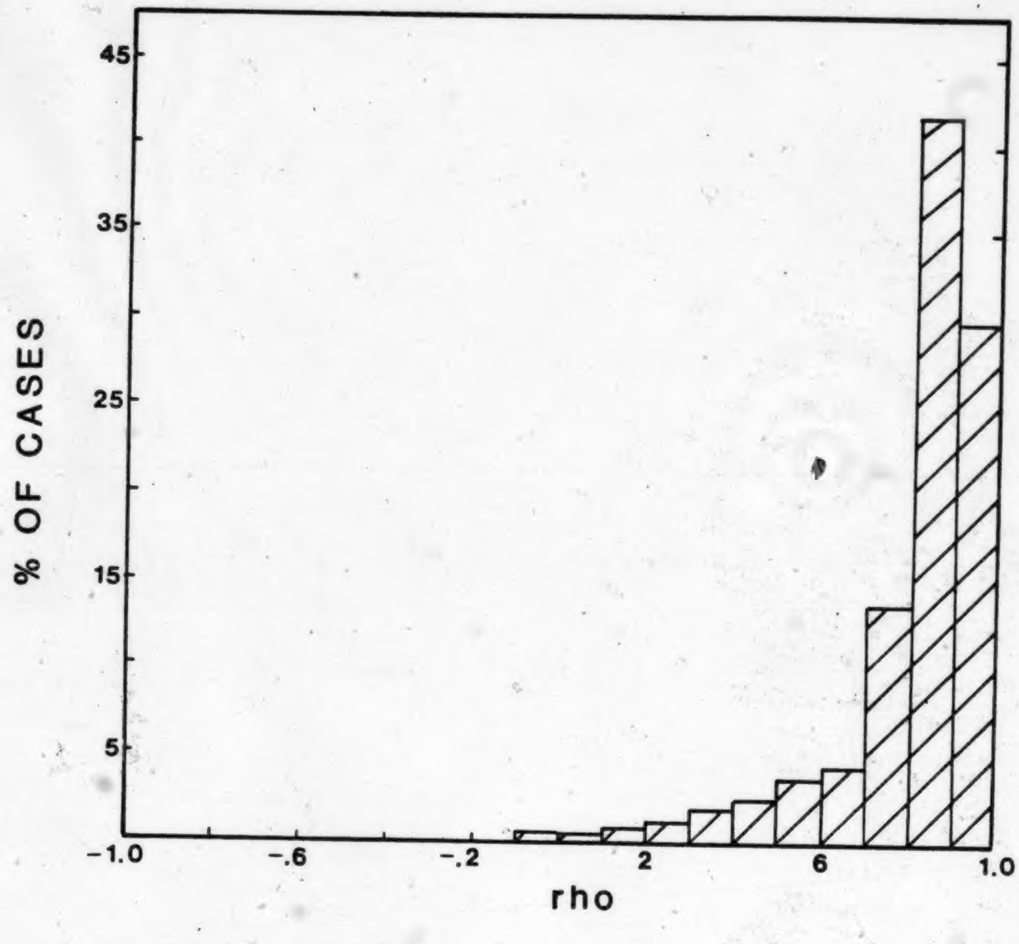

45
35
25
15
5
% OF CASES
-1.0
-.6
-.2
2
6
1.0
rho

Table 7. Spearman rank correlations of positions of helminths in the intestines of four species of grebes.

	Aechmophorus occidentalis	*Podiceps grisegena*	*Podiceps nigricollis*	*Podiceps auritus*
No. of Comparisons	53	490	388	5
No. of Significant Comparisons ($P \leq .05$)	17	319	310	3
% Significant	32	65	80	60
Mean rho (SD)	.714 (.234)	.756 (.183)	.839 (.193)	.851 (.123)

Because distributions of species may be sensitive to the size of their infrapopulations, rank correlations between the positions of the first, last, and medianth individuals, as well as the range occupied by each helminth and intensity in each infracommunity were calculated (Tables 8-11). The size of the infrapopulation seldom affected the location of the medianth individual; in only 6 of 51 (12%) of the helminths in the four grebe species was the location significantly ($P<.05$) related to population size. Five of these six species moved posteriad (*i.e.*, towards the ileo-caecal junction) in conjunction with increasing populations while only *Schistotaenia srivastavai*, in *P. auritus*, moved anteriad (*i.e.*, towards the pyloric sphincter) (Tables 8 to 11). Six of 51 (22%) of the last individuals were more posteriad (none moved forward).

The ranges of helminths in the intestines of grebes were more sensitive to infrapopulation size. There was a significant expansion for 20 of 48 (42%) of the species, while 94% had positive correlations. Although the order of occurrence and positions of helminths, as measured by the locations of the medianth individuals, were predictable and usually refractory to increasing infrapopulation sizes, the ranges of the parasites generally expanded when infrapopulations increased in size.

Total occupied ranges for core species (Fig. 8; Tables 3-6) were generally over 60% of the intestinal length (21 of 32 cases), with 14 of these over 90%. Most species (9/16)

Table 8. Effect of increasing population size on distributional characteristics of helminths in Aechmophorus occidentalis.

Helminth	Effect on:			
	Median	Anterior	Posterior	Range
Tylodelphys podicipina*	0	0	0	0
Tatria biremis	0	A	0	0
Dubininolepis furcifera*	0	0	0	0
Petasiger nitidus*	0	0	0	0
Apatemon gracilis	0	0	0	0
Wardium paraporale*	0	0	P	+
Ligula intestinalis*	0	0	0	+
Tetrabothrius immerinus	0	0	0	0
Schistocephalus solidus	0	0	0	++

* = core species

0 = no effect

A = moved anteriad, P < .05

P = moved posteriad, P < .05

+ = expanded range, P < .05

++ = expanded range, P < .01

Table 9. Effect of increasing population size on distributional characteristics of helminths in *Podiceps grisegena*.

Helminth	Effect on:			
	Median	Anterior	Posterior	Range
Pararetinometra lateralacantha	PP	0	0	+
*Tylodelphys podicipina**	PP	0	PP	++
*Dubininolepis furcifera**	0	0	PP	++
*Tatria biremis**	0	0	0	0
*Schistotaenia srivastavai**	0	0	P	++
*Petasiger nitidus**	0	A	PP	++
*Tatria decacantha**	0	0	0	++
*Wardium paraporale**	0	0	0	++
Apatemon gracilis	0	0	0	0
*Contracaecum ovale**	0	A	0	0
*Dioecocestus asper**	0	0	0	0
Tetrabothrius immerinus	0	0	0	0
immature strigeids	0	0	0	0
Ligula intestinalis	0	0	0	++
*Capillaria obsignata**	0	0	0	+
Schistocephalus solidus	0	0	0	0

* = core species

0 = no effect

A = moved anteriad, $P < .05$

P = moved posteriad, $P < .05$

PP = moved posteriad, $P < .01$

+ = expanded range, $P < .05$

++ = expanded range, $P < .01$

Table 10. Effect of increasing population size on distributional characteristics of helminths in Podiceps nigricollis.

Helminth	Effect on: Median	Anterior	Posterior	Range
Nadejdolepis sp.	0	0	PP	++
Dubininolepis furcifera	0	0	0	0
Diorchis sp. O*	PP	0	PP	++
Tatria biremis*	0	0	0	0
Petasiger nitidus	0	0	0	++
Schistotaenia colymba	0	A	PP	+
Apatemon gracilis	0	0	0	0
Microsomacanthus sp. T	0	0	0	0
Dubininolepis podicipina*	0	0	0	0
Contracaecum ovale	0	A	0	++
Diorchis sp. P*	0	A	PP	++
Tatria decacantha*	P	0	P	0
Lateriporus skrjabini	0	0	0	0
Capillaria obsignata	0	0	0	0
Wardium paraporale*	0	0	0	0
Microsomacanthus sp. Z	0	0	0	0

* = core species

0 = no effect

A = moved anteriad, $P < .05$

P = moved posteriad, $P < .05$

PP = moved posteriad, $P < .01$

+ = expanded range, $P < .05$

++ = expanded range, $P < .01$

Table 11. Effect of increasing population size on distributional characteristics of helminths in *Podiceps auritus*.

Helminth	Effect on:			
	Median	Anterior	Posterior	Range
Dubininolepis furcifera	PP	0	PP	++
Schistotaenia srivastavai	A	0	0	--
*Tatria biremis**	0	0	0	0
Petasiger nitidus	0	0	0	0
Tatria decacantha	0	0	0	0
Contracaecum ovale	0	0	0	++
*Wardium paraporale**	0	0	0	0
Tetrabothrius immerinus	0	0	0	0

* = core species

0 = no effect

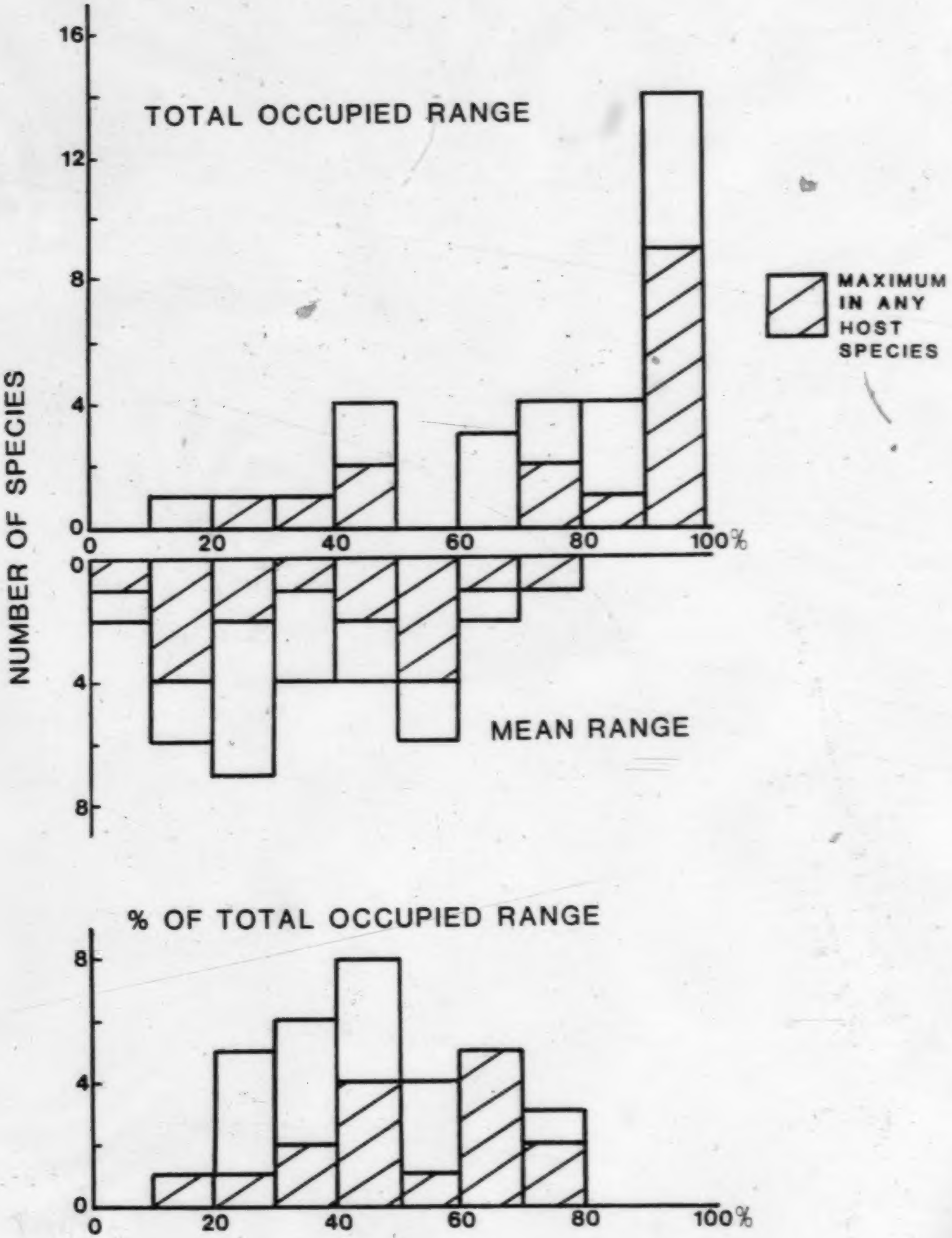
A = moved anteriad, $P < .05$

PP = moved posteriad, $P < .01$

++ = expanded range, $P < .01$

-- = contracted range, $P < .01$

Figure 8. Frequency distributions of core helminth species based on their total occupied ranges, mean ranges and the proportion of the total occupied range that the mean range represents.


TOTAL OCCUPIED RANGE
MEAN RANGE
% OF TOTAL OCCUPIED RANGE
NUMBER OF SPECIES
MAXIMUM IN ANY HOST SPECIES
0
4
8
12
16
0
4
8
0
4
8
0
20
40
60
80
100%

occupied over 90% of the intestine in at least one host species. If this measure is considered the best estimate of the fundamental niche, most core species had fundamental niches that encompassed almost the entire small intestine. They showed great adaptability, indicative of broad tolerance. Only a few species of cestodes, notably the species of *Schistotaenia*, which had maximum ranges equal to or less than one-third of the length of the intestine, appeared to be limited by their tolerance to intestinal conditions.

Realized niches were considerably smaller. Mean ranges were 17 to 76% (mean:46%) of the total occupied ranges (Fig. 8). If reductions were due solely to small infrapopulations, then little variance about the mean of the median positions, and little variance in the mean median positions of helminths in different grebe species would be expected. Neither was true. While half of the core species showed small standard deviations (<10% of the intestinal length), ten of the cases showed standard deviations of more than 15% (Fig. 9). In addition, the positions of nine of the 13 core species that occurred in two or more species of hosts, varied significantly in position among hosts (Table 12, Fig. 10). These analyses suggest that, although the intestinal helminths in grebes are potentially capable of inhabiting large areas within the intestine, they actually reside in smaller, more localized regions that may differ among different host species, or among individuals of the same

Figure 9. Frequency distribution of the standard deviations of mean median positions of core helminth species in four species of grebes.

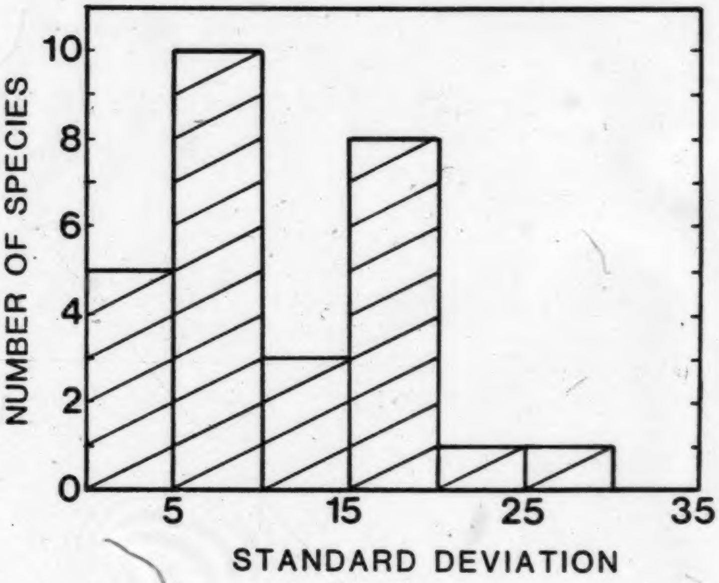
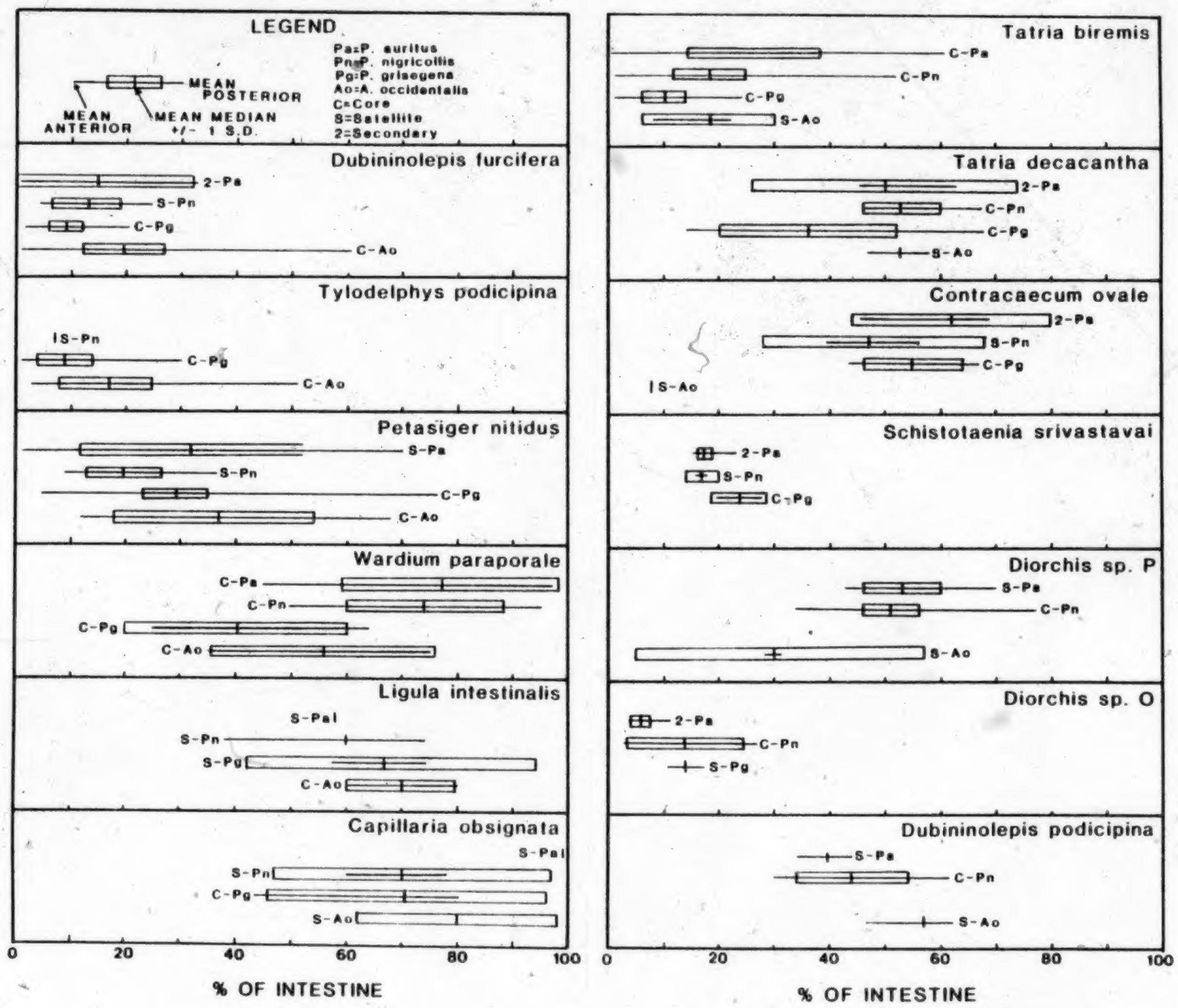

NUMBER OF SPECIES
0
2
4
6
8
10
5
15
25
35
STANDARD DEVIATION

Table 12. Summary of one-way ANOVA comparing distributions of medians between hosts to those within hosts.

Helminth	Degrees of Freedom	F-Statistic	Significance
Dubininolepis furcifera	3,58	9.975	.0000
Petasiger nitidus	3,52	2.837	.0469
Wardium paraporale	3,84	20.853	.0000
Capillaria obsignata*	3,49	0.851	.4727
Tylodelphys podicipina	2,44	5.099	.0102
Tatria biremis	3,69	13.377	.0000
Ligula intestinalis	3,24	0.293	.8301
Contracaecum ovale	3,46	4.307	.0093
Tatria decacantha	3,53	7.524	.0003
Diorchis "P"	2,25	9.538	.0008
Dubininolepis podicipina	2,28	0.798	.4603
Schistotaenia srivastavai	2,27	4.343	.0232
Diorchis "O"	2,27	0.603	.5542

Figure 10. Distribution of core, secondary and recurrent group helminths in four species of grebes.


LEGEND
MEAN POSTERIOR
MEAN ANTERIOR
MEAN MEDIAN +/- 1 S.D.
Pa=P. auritus
Pn=P. nigricollis
Pg=P. grisegena
Ao=A. occidentalis
C=Core
S=Satellite
2=Secondary
Dubininolepis furcifera
2-Pa
S-Pn
C-Pg
C-Ao
Tylodelphys podicipina
S-Pn
C-Pg
C-Ao
Petasiger nitidus
S-Pa
S-Pn
C-Pg
C-Ao
Wardium paraporale
C-Pa
C-Pn
C-Pg
C-Ao
Ligula intestinalis
S-Pal
S-Pn
S-Pg
C-Ao
Capillaria obsignata
S-Pal
S-Pn
C-Pg
S-Ao
0
20
40
60
80
100
% OF INTESTINE
Tatria biremis
C-Pa
C-Pn
C-Pg
S-Ao
Tatria decacantha
2-Pa
C-Pn
C-Pg
S-Ao
Contracaecum ovale
2-Pa
S-Pn
C-Pg
S-Ao
Schistotaenia srivastavai
2-Pa
S-Pn
C-Pg
Diorchis sp. P
S-Pa
C-Pn
S-Ao
Diorchis sp. O
2-Pa
C-Pn
S-Pg
Dubininolepis podicipina
S-Pa
C-Pn
S-Ao
0
20
40
60
80
100
% OF INTESTINE

host species. These reductions can not be attributed solely to reduced infrapopulations, thus suggesting interactive forces.

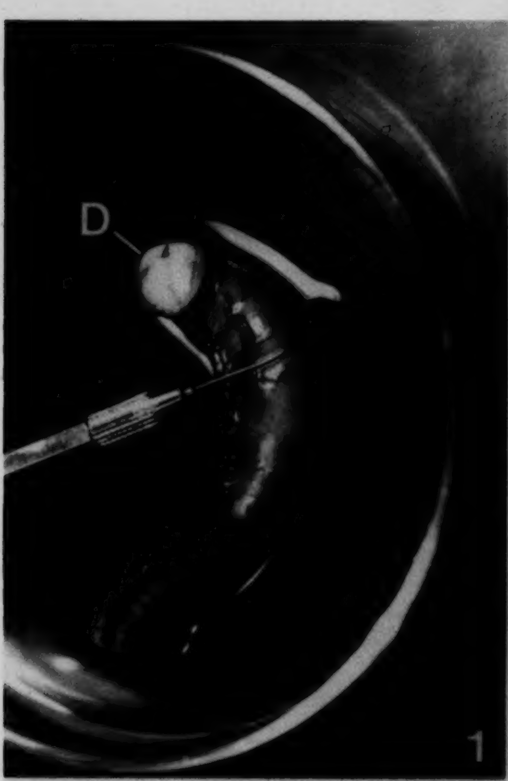
When helminths were core species in both *P. grisegena* and other grebes, they had more anteriad distributions in *P. grisegena*: *D. furcifera*, *Tylodelphys podicipina*, *Petasiger nitidus*, and *Wardium paraporale* were more anteriad when in *P. grisegena* than in *A. occidentalis*; *W. paraporale*, *Tatria biremis* and *Tatria decacantha* were more anteriad in *P. grisegena* than in *P. nigricollis* or *P. auritus*. (Fig. 10).

Consistent differences in physico-chemical conditions in the luminal and mucosal environments among grebes (particularly between *P. grisegena* and the other grebes), could account for such a pattern. However, when helminths occurred as secondary or satellite species in grebes other than *P. grisegena*, they occasionally were more anteriad in position in those grebes. For example, *Schistotaenia srivastavai* was more anteriad in both *P. nigricollis* and *P. auritus*, and *Tylodelphys podicipina* and *Petasiger nitidus* were both more anteriad in *P. nigricollis*. In addition, if one assumes that the position of a species in the major or required host (that host that maintains the bulk of the parasite's breeding population) is optimal for that helminth, then examination of its distribution in other hosts should reveal consistent anteriad or posteriad shifts if physico-chemical conditions vary uniformly. No such consistent shifts were noted. These observations suggest that there were no uniform physico-chemical differences between the intestines of *P. grisegena* and the other hosts that might account for the consistent anterior positioning of shared core species, and that some other factor must be involved.

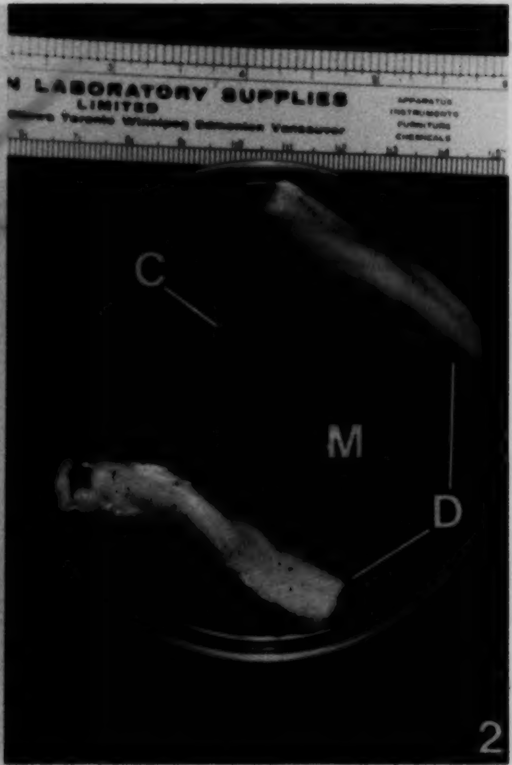
Dioecocestus asper is a core species of *P. grisegena* that resides in the mid-intestine (mean position: 54%). Besides being strictly host-species specific, *D. asper* is unusual in that it is a truely dioecious cestode (the Dioecocestidae and Gyrocoelidae are the only completely dioecious tapeworms known, Tolkacheva, 1983), usually (24/27 cases) found within a host as a mixed-sex pair. Stringent population regulation occurs. Immature worms have scolices armed with large rostellar hooks. Hooks are lost as the worms mature in the definitive host and *D. asper* uses its large size to retain its position in the intestine. Despite low infrapopulation densities, *D. asper* has significant effects on the host intestine (Fig. 11), probably due to its bulk. Total biomass of *D. asper*, as measured by wet weight, ranged from 0.5 g to 13.7 g, with a mean of 8.8 g. Histological sections showed that segments of the intestine infected with *D. asper* sustained severe damage to the mucosal surface including flattening and erosion of villi characteristic of pressure necrosis (Figs. 11-13). In addition, mature *D. asper* infections created intestinal blockages with plugs of green luminal contents and mucous. Segments of intestine with *D. asper* were radially stretched,

Figure 11. Dioecocestus asper in the intestine of Podiceps grisegena.

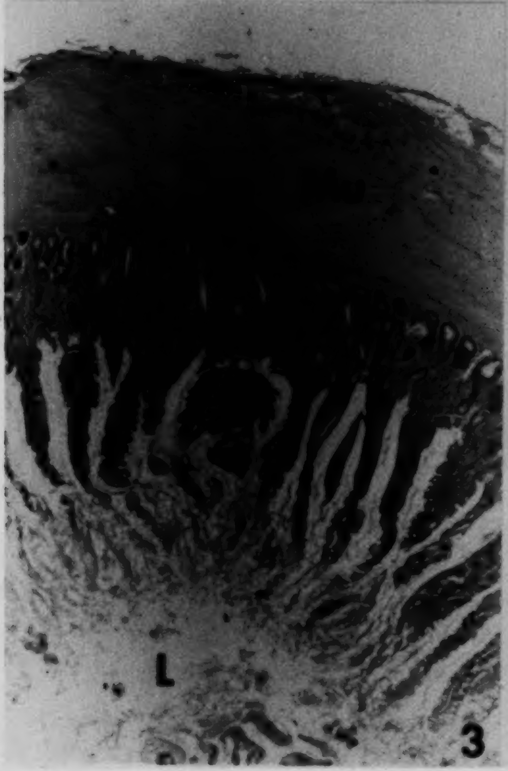
1. Gross view of intestinal section 11 containing D. asper (= D).
2. Intestinal section 11, after being split open to reveal the strobilae of a male and a female D. asper. Note creases on the mucosal surface (M), resulting from the ascarid nematode, Contracaecum ovale (C) being pressed into the mucosa by D. asper (D).
3. Transverse histological section of intestinal segment 11 from a grebe that was not infected with D. asper. Mu = muscularis, M = mucosa, L = lumen, T = Tatria decacantha, a smaller tapeworm attached to the mucosa.
4. Transverse histological section of intestinal segment 11 from a grebe infected with D. asper. M = mucosa, D = D. asper.


D

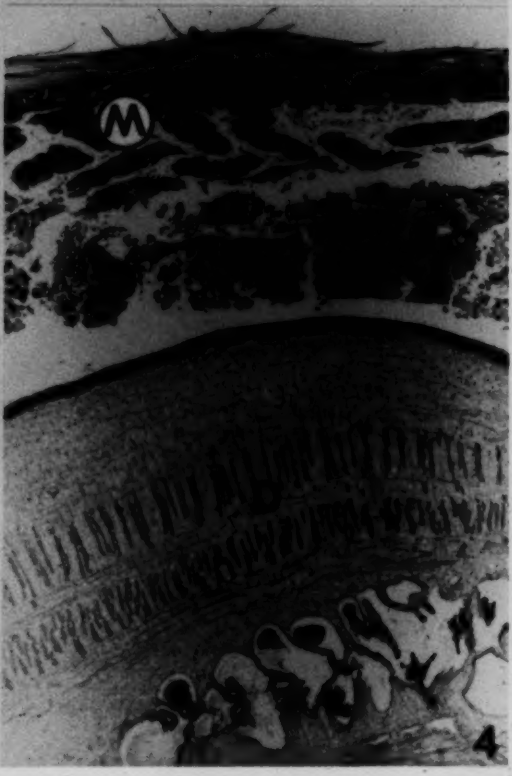
1


N LABORATORY SUPPLIES
LIMITED
Ottawa Toronto Winnipeg Edmonton Vancouver
APPARATUS
INSTRUMENTS
FURNITURE
CHEMICALS
C
M
D

2


L

3


M

4

Figure 12. Mucosal widths of intestinal sections in *Podiceps grisegena* infected with (dashed lines) and without (solid line) *Dioecocestus asper*.

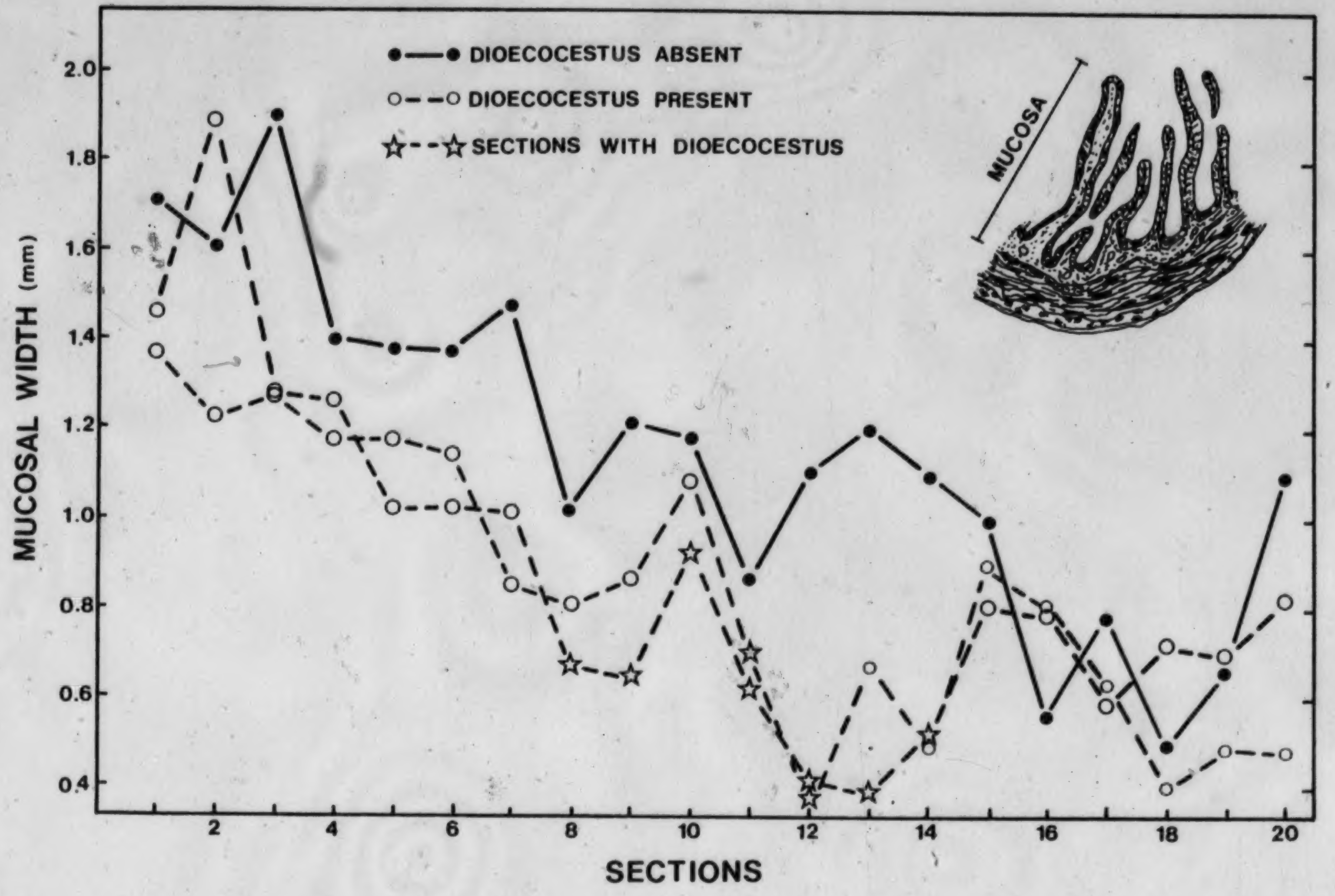
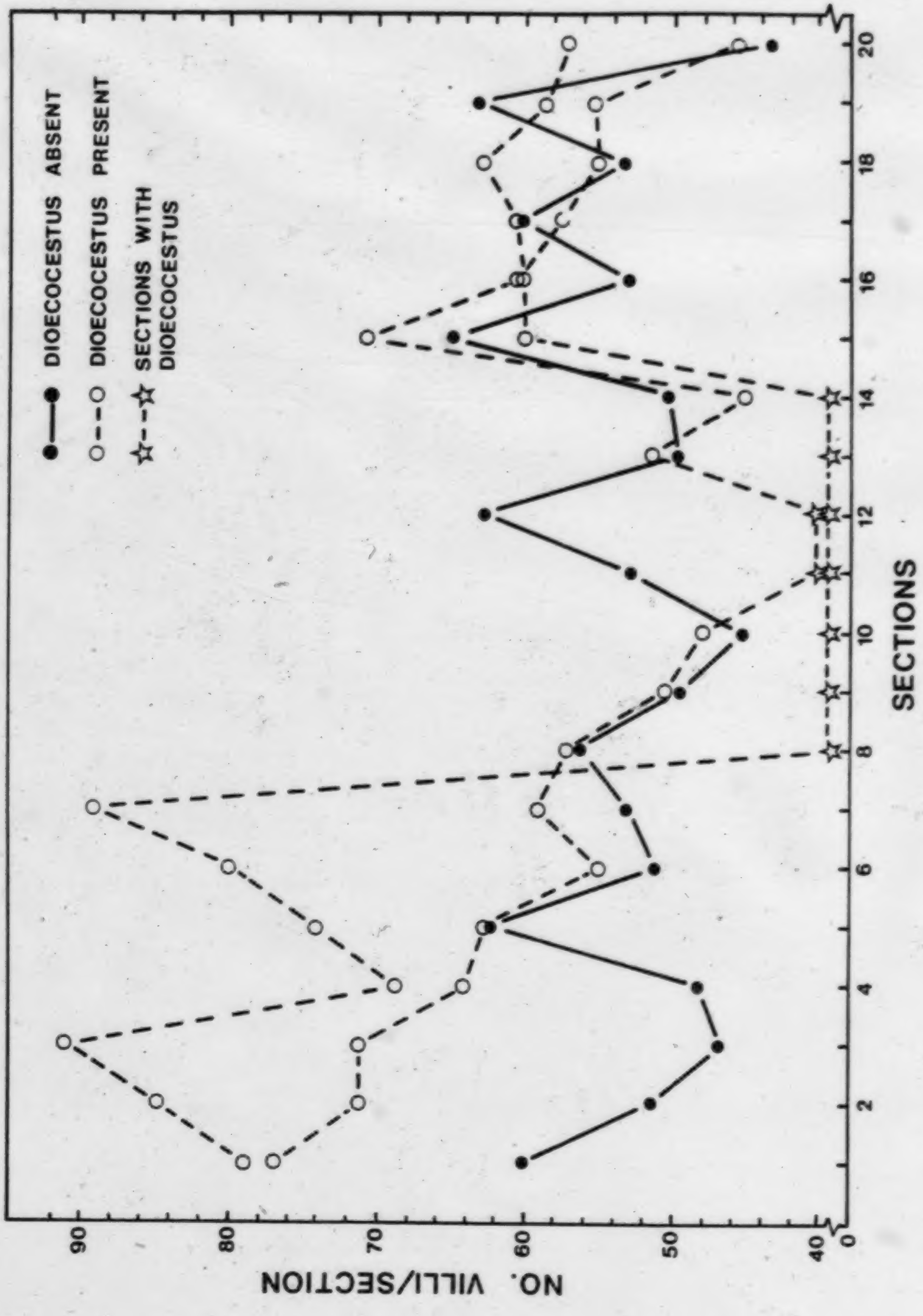

● — ● DIOECOCESTUS ABSENT
○ - - ○ DIOECOCESTUS PRESENT
☆ - - ☆ SECTIONS WITH DIOECOCESTUS
MUCOSA
MUCOSAL WIDTH (mm)
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
2
4
6
8
10
12
14
16
18
20
SECTIONS

Figure 13. Mean number of villi per intestinal section in *Podiceps grisegena* infected with (dashed lines) and without (solid line) *Dioecocestus asper*.

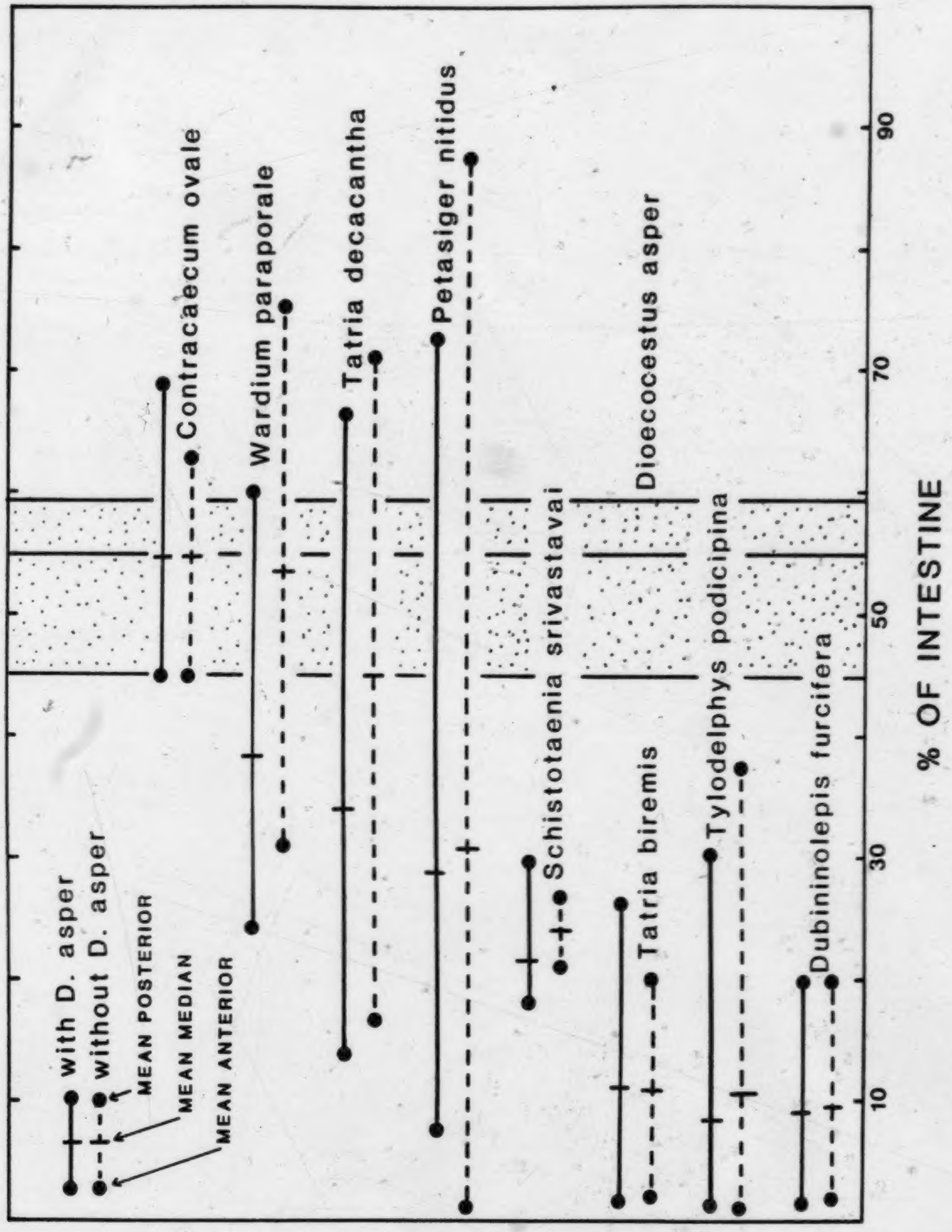

DIOECOCESTUS ABSENT
DIOECOCESTUS PRESENT
SECTIONS WITH DIOECOCESTUS
NO. VILLI/SECTION
SECTIONS
90
80
70
60
50
40
0
2
4
6
8
10
12
14
16
18
20

(to more than 150% of normal, 11.3 mm *vs.* 7.3 mm), to the point where worms were plainly visible through the intestinal wall. Grossly, the mucosa had "tire-track" patterning that corresponded to the imprint of the *D. asper* proglottids. One, and possibly both, of the infected birds examined histologically demonstrated a compensatory increase in the number of villi in intestinal segments anterior to *D. asper* infections.

The presence of *D. asper* markedly affected other helminths. Six of seven core helminths with positions anterior to *D. asper* had more anterior mean positions (but not significantly so) in infections where *D. asper* was present (Fig. 14). Those species with positions closest to *D. asper*, *Wardium paraporale* and *Tatria decacantha* had the greatest shift (t-test, t= 1.89, df=29, .05<P<.10 for *W. paraporale*; t= 1.48, df=25, .10<P<.15 for *T. decacantha*). Increasing wet weight of *D. asper* was correlated with a significant anteriad shift in the position of *Schistotaenia srivastavai* (product moment correlation, r= -.747, df=16, P< .01), and suggested forward shifts in the position of *Tatria biremis* (r= -.409, df=19, .05<P<.10) and the posterior most *Tatria decacantha* (r= -.321, df=16, .10<P<.20). The data suggest, but do not clearly demonstrate, that other species react to the presence and amount of *D. asper* by shifting their position in the intestine.

D. asper was clearly associated with a significant reduction in the mean number of species per bird (12.3 *vs.*

Figure 14. Distribution of core species of _Podiceps_ _grisegena_ in infections with, and without _Dioecocestus_ _asper_. _Capillaria_ _obsignata_ is omitted because most specimens occurred in the caeca.


with D. asper
without D. asper
MEAN POSTERIOR
MEAN MEDIAN
MEAN ANTERIOR
Contracaecum ovale
Wardium paraporale
Tatria decacantha
Petasiger nitidus
Schistotaenia srivastavai
Dioecocestus asper
Tatria biremis
Tylodelphys podicipina
Dubininolepis furcifera
10
30
50
70
90
% OF INTESTINE

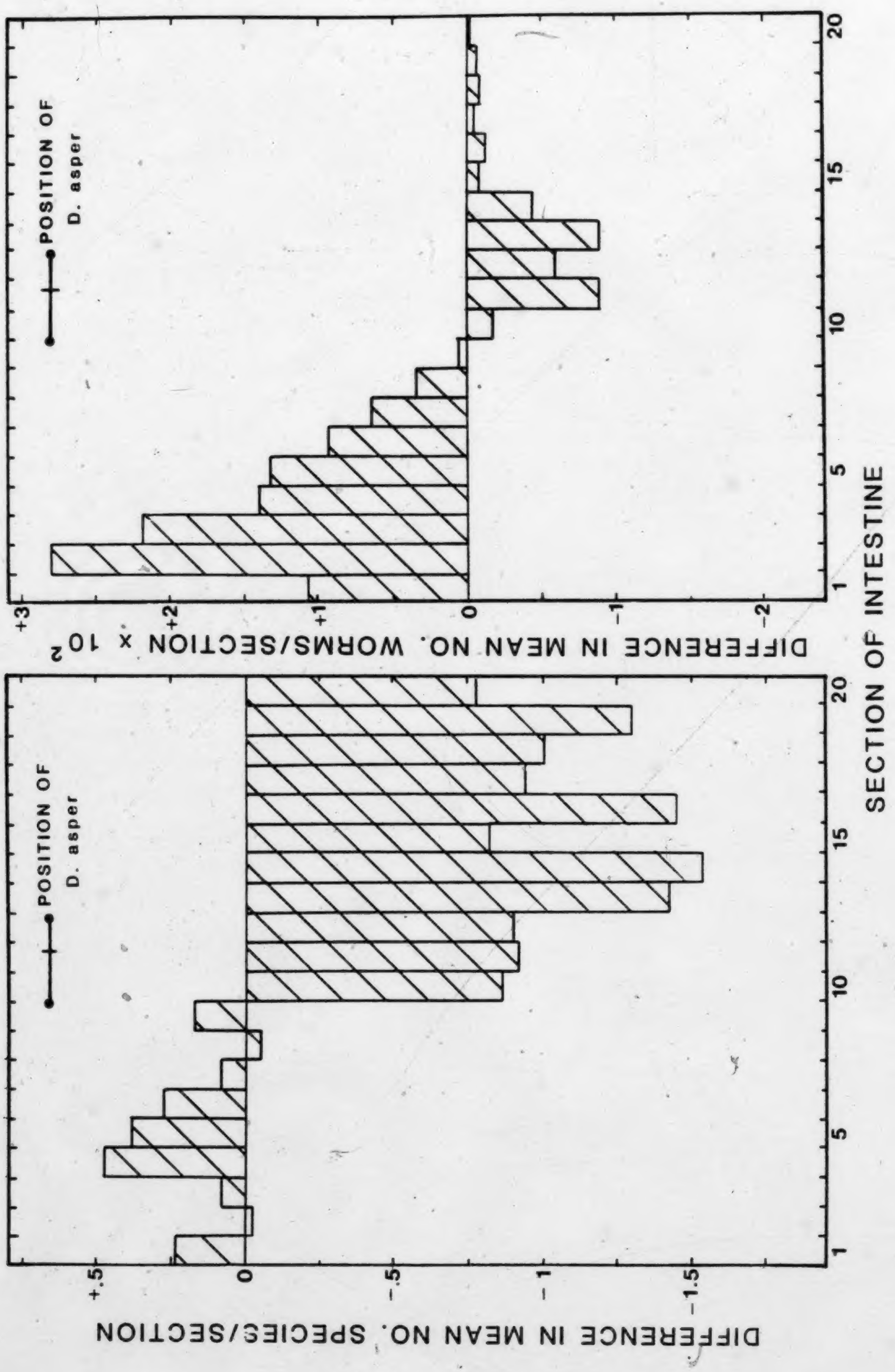
9.6, t=3.88, df=31, P<.001). In addition, both the mean number of species and the mean number of worms per intestinal section (Fig. 15) seem to be affected. There may be a compensatory increase in species and numbers in the sections anterior to *D. asper*.

One core parasite of *P. grisegena*, *Contracaecum ovale*, had a distribution that was virtually identical to that of *D. asper* (Fig. 11). The position of the medianth individual of *C. ovale* was positively correlated with the median position (based on the distribution of wet weight) of *D. asper* (r= .723, df=16, P<.001). Frequently, *C. ovale* were pressed into the mucosal surface by *D. asper* (Fig. 12). *C. ovale* is a large, robust ascarid nematode that feeds on host luminal contents. *C. ovale* may benefit from the intestinal blockage created by *D. asper*; however, in infections without *D. asper*, *C. ovale* occurred in the same location. No intestinal pathology was noted when *C. ovale* occurred without *D. asper*.

Therefore, the distributions of some core helminths in *P. grisegena*, species richness and intensity per intestinal segment appear to be affected by the presence in the mid-intestine of *D. asper* and by the pathology that it causes.

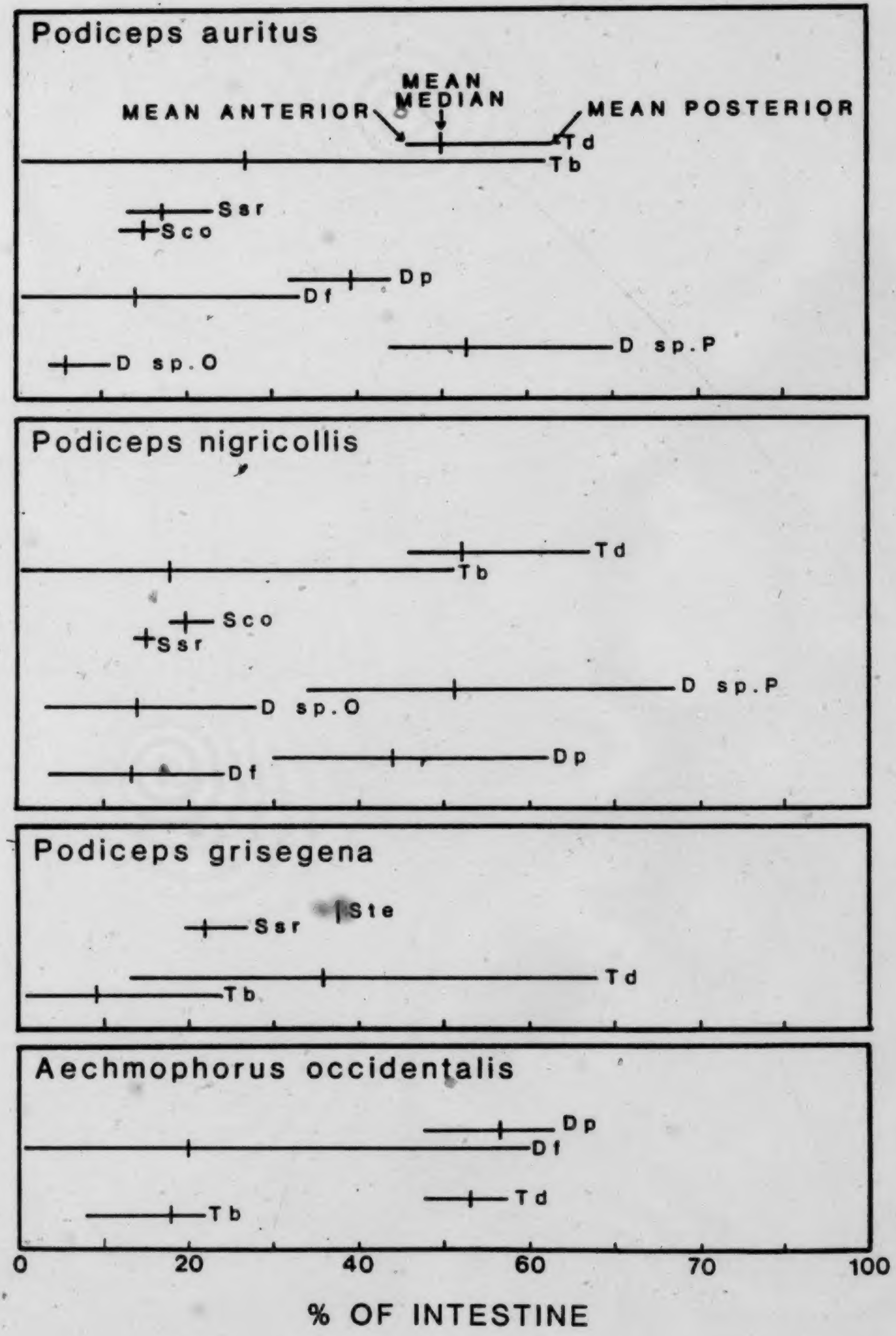
Five sets of congeners, all cestodes, occurred in these grebes: *Tatria biremis* and *T. decacantha* co-occurred in all four host species, *Dubininolepis furcifera* and *D. podicipina* co-occurred in all but *P. grisegena*, *Diorchis* sp. 0 and

Figure 15. The differences in the mean number of helminth species, and the mean number of individual worms, in sections of intestine with and without Dioecocestus asper.


DIFFERENCE IN MEAN NO. SPECIES/SECTION
+.5
0
-.5
-1
-1.5
POSITION OF
D. asper
DIFFERENCE IN MEAN NO. WORMS/SECTION x 10²
+3
+2
+1
0
-1
-2
POSITION OF
D. asper
1
5
10
15
20
SECTION OF INTESTINE

Diorchis sp. P and *Schistotaenia colymba* and *S. srivastavai* co-occurred in *P. nigricollis* and *P. auritus*, and *S. srivastavai* co-occurred with a single individual of *S. tenuicirrus* in *P. grisegena*. In six of 12 cases, the congeners demonstrated largely disjunct distributions (average ranges, as indicated by mean posterior position of the anterior species and the mean anterior position of the posterior species do not overlap) (Fig. 16). In three others, ranges overlap, but mean positions are in non-overlapping portions of the ranges. Two (the two *Tatria* spp. in *P. auritus* and the two *Dubininolepis* spp. in *A. occidentalis*) had broadly overlapping ranges but widely separated mean positions. Only *S. colymba* and *S. srivastavai* in *P. auritus* had essentially the same ranges and mean positions; they did not co-occur in the same host individual. The distributions of these two species were particularly interesting. *S. srivastavai* occurred predominently in *P. grisegena* (94% of all individuals) while 98% of *S. colymba* infected *P. nigricollis*. In their usual hosts, the two species occupied essentially the same areas. However, when *S. srivastavai* occurred in *P. nigricollis*, its position was displaced anteriorly. Both *S. colymba* and *S. srivastavai* occurred more forward in *P. auritus* than in their main hosts (15% *vs.* 23% for *S. srivastavai*; 17% *vs.* 21% for *S. colymba*). Although these events occurred too rarely to be statistically analyzed, the median position of either species in grebes other than its main host lay

Figure 16. The distributions of pairs of congeneric helminths in four species of grebes.


Podiceps auritus
MEAN
MEDIAN
MEAN ANTERIOR
MEAN POSTERIOR
Td
Tb
Ssr
Sco
Dp
Df
D sp.P
D sp.O
Podiceps nigricollis
Td
Tb
Sco
Ssr
D sp.P
D sp.O
Dp
Df
Podiceps grisegena
Ste
Ssr
Td
Tb
Aechmophorus occidentalis
Dp
Df
Td
Tb
0
20
40
60
70
100
% OF INTESTINE

outside the standard deviation of the mean median in its main host. The two species of *Schistotaenia* differed primarily in host specificity, but had similar distributions in their main hosts; in other hosts, each assumed a more anterior position.

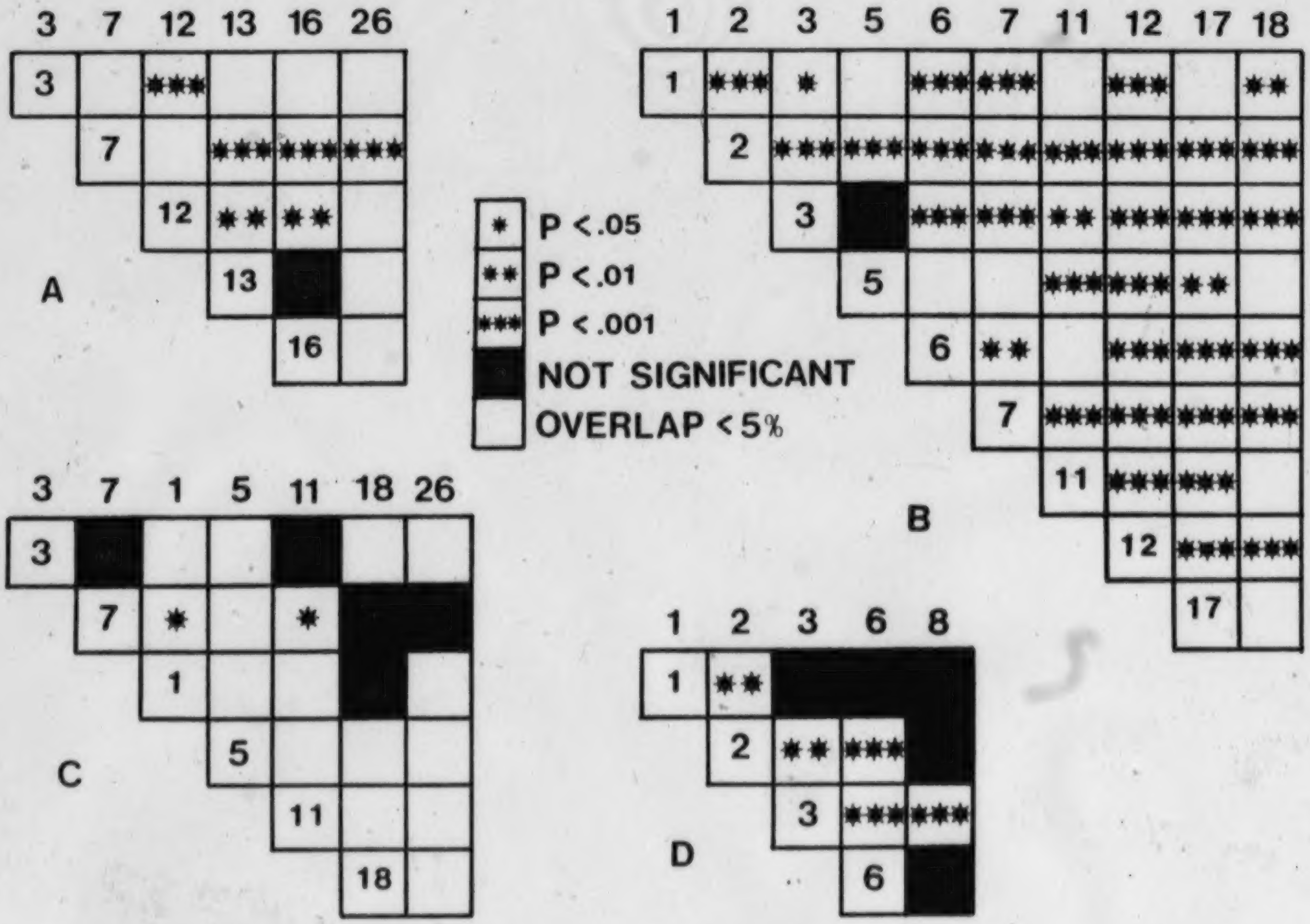
The remaining sets of congeners usually co-occur. Two sets, *Dubininolepis* spp., and *Diorchis* spp., were recurrent group species in *P. nigricollis* only (see Chapt. 2), while *Tatria biremis* and *T. decacantha* together were included in the recurrent groups of *P. grisegena* and *P. nigricollis*. All demonstrated complementarity of distribution with little overlap, as measured by percent similarity (15% for *T. biremis* and *T. decacantha* in *P. grisegena* and 3% in *P. nigricollis*; 7% for *D. furcifera* and *D. podicipina*; and 0.4% for *Diorchis* sp. O and sp. P). The species of *Tatria* also demonstrated complementarity of numbers in *P. grisegena* and *P. nigricollis*. In *P. grisegena*, *T. biremis* had a mean intensity of 377 and *T. decacantha* a mean intensity of 1085; in *P. nigricollis*, however, *T. biremis* had a mean intensity of 2794 and *T. decacantha*, 53. In *P. grisegena*, its main host, increasing numbers of *T. decacantha* were correlated with a significant reduction in the ranges of the more anteriorly positioned *T. biremis* ($r= -.392$, $df=30$, $.01<P<.05$). This effect was not seen in *P. nigricollis*. In *P. nigricollis*, *Diorchis* sp. P was found in the mid-intestine (mean median = 51%). Overlap with its congener, *Diorchis* sp. O was small, 0.4%, and no correlations between them indicative of interaction were noted. *Diorchis* sp. P did have a significant effect on two other species. Increasing numbers of *Diorchis* sp. P were associated with posterior shifts in the anterior most and median individuals of *Wardium paraporale* ($r= .360$, $df=29$, $P<.05$; and $r= .324$, $df=29$, $.05<P<.10$, respectively) and *T. decacantha* ($r= .569$, $df=21$, $P<.01$; and $r= .783$, $df=21$, $P<.001$, respectively). *P. nigricollis* is not the main host for either *W. paraporale* or *T. decacantha*. No signs of interaction were noted between the species of *Dubininolepis* in *P. nigricollis*. As between the *Diorchis* congeners, overlap was small. Therefore, congeners specialized in habitat use in different ways. *Schistotaenia* species were host species specialists, *Diorchis* and *Dubininolepis* species were microhabitat specialists and *Tatria* species combined microhabitat separation with concentration in different host species.

As demonstrated by *D. asper* and *Diorchis* sp. P, distributional patterns of species other than congeners can indicate interactions. One method of scanning for such interactions is to look for significant reductions in the overlaps between the realized niches, compared with the overlaps between the fundamental niches, of pairs of species. The lack of a reduction is suggestive of no interaction. Overlaps in the fundamental niches of all pairs of core species were calculated using percent similarity of distributions (Bush, 1980; Butterworth, 1982); overlaps in realized niches (in the same bird) were calculated in the same way. For each pair of species, the overlap in fundamental niches was compared with the average overlap in realized niches by a t-test. Species pairs with overlaps in fundamental niches of less than 5% were disregarded. Overlaps in realized niches were significantly reduced ($P<.05$) in many of the species pairs (35/36 for *P. grisegena*, 6/7 for *P. nigricollis*, and 5/10 for *A. occidentalis*; but only 2/7 in *P. auritus*, in which sample sizes were very small) (Fig. 17).

Almost all helminth species had expanded ranges when their population sizes were large. Therefore, the overlap between any two species would be expected to increase when joint population sizes of the two were high, unless the two were avoiding overlap. However, overlap between pairs of recurrent group species seldom showed a significant correlation with their combined population densities (Fig. 18). In four of seven cases in which there was a significant correlation (those involving *Petasiger nitidus* or *Capillaria obsignata*) the species use intestinal resources differently. *Petasiger nitidus* is a trematode that engulfs host tissue and is closely associated with the mucosal surface; in *P. grisegena* it had increased overlap with three cestodes, *Dubininolepis furcifera*, *Tatria decacantha*, and *Schistotaenia srivastavai*, which absorb nutrients from the luminal contents. *Petasiger nitidus* did not have increased overlap with the other common trematode, *Tylodelphys*

Figure 17. Reductions in overlaps of realized niches of core helminths in four species of grebes. A = *Podiceps nigricollis*, B = *Podiceps grisegena*, C = *Podiceps auritus*, D = *Aechmophorus occidentalis*.

1 = *Dubininolepis furcifera*, 2 = *Petasiger nitidus*,
3 = *Wardium paraporale*, 5 = *Capillaria obsignata*,
6 = *Tylodelphys podicipina*, 7 = *Tatria biremis*,
8 = *Ligula intestinalis*, 11 = *Contracaecum ovale*,
12 = *Tatria decacantha*, 13 = *Diorchis* sp. P,
16 = *Dubininolepis podicipina*, 17 = *Dioecocestus asper*,
18 = *Schistotaenia srivastavai*, 26 = *Diorchis* sp. O.



3	7	12	13	16	26
3		***			
	7		***	***	***
		12	**	**	
			13	■	
				16	

A

1	2	3	5	6	7	11	12	17	18
1	***	*		***	***		***		**
	2	***	***	***	***	***	***	***	***
		3	■	***	***	**	***	***	***
			5			***	***	**	
				6	**		***	***	***
					7	***	***	***	***
						11	***	***	
							12	***	***
								17	

B

3	7	1	5	11	18	26
3	■			■		
	7	*		*	■	■
		1			■	
			5			
				11		
					18	

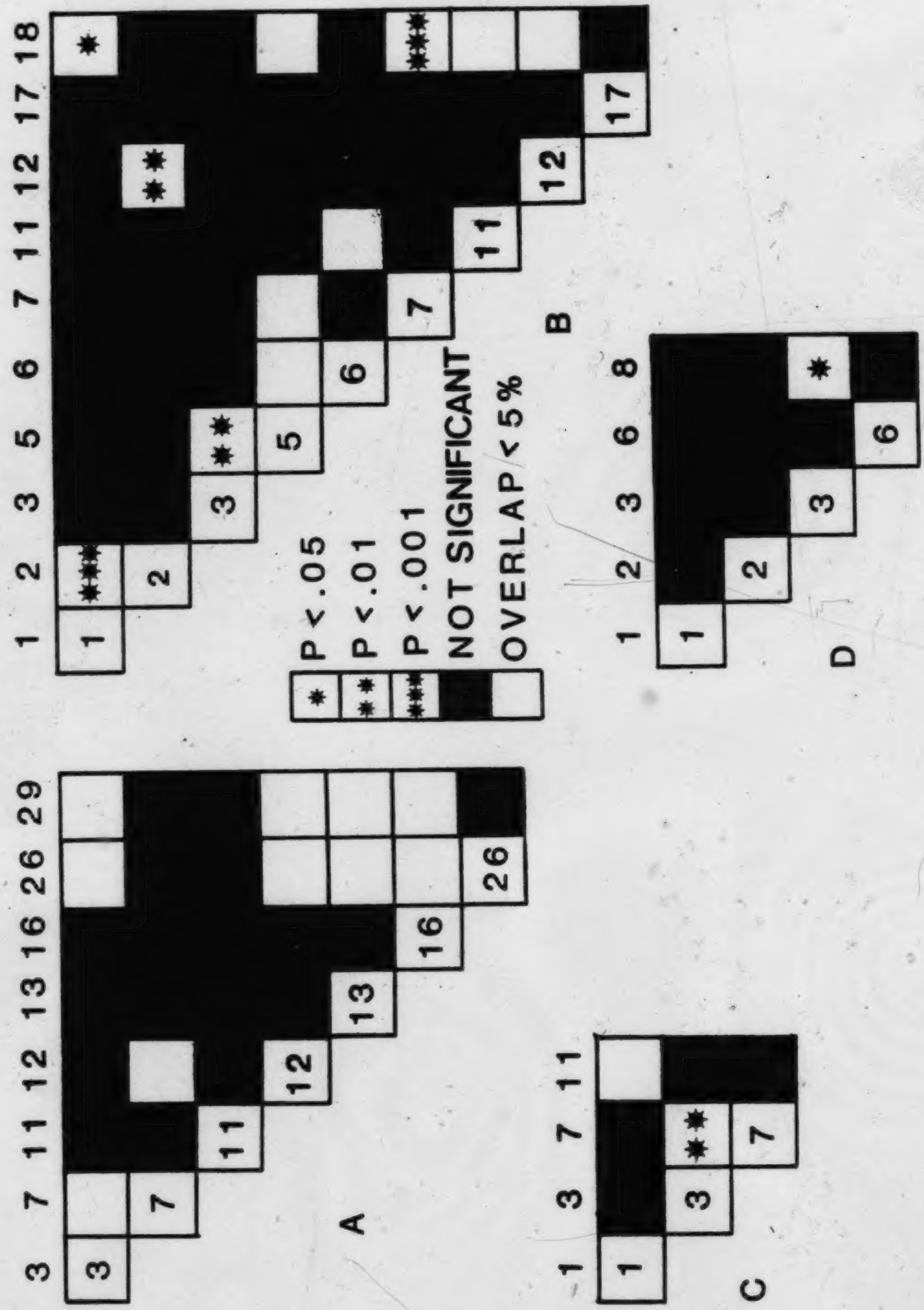
C

1	2	3	6	8
1	**	■	■	■
	2	**	***	■
		3	***	***
			6	■

D

*	P <.05
**	P <.01
***	P <.001
■	NOT SIGNIFICANT
	OVERLAP <5%

Figure 18. Significant increases in overlap with increasing combined population sizes. A = Podiceps nigricollis,
B = Podiceps grisegena, C = Podiceps auritus,
D = Aechmophorus occidentalis.
1 = Dubininolepis furcifera, 2 = Petasiger nitidus,
3 = Wardium paraporale, 5 = Capillaria obsignata,
6 = Tylodelphys podicipina, 7 = Tatria biremis,
8 = Ligula intestinalis, 11 = Contracaecum ovale,
12 = Tatria decacantha, 13 = Diorchis sp. P,
16 = Dubininolepis podicipina, 17 = Dioecocestus asper,
18 = Schistotaenia srivastavai, 26 = Diorchis sp. O,
29 = Schistotaenia colymba.


A
3 7 11 12 13 16 26 29
B
1 2 3 5 6 7 11 12 17 18
C
1 3 7 11
D
1 2 3 6 8
P < .05
P < .01
P < .001
NOT SIGNIFICANT
OVERLAP < 5%

podicipina. Instead, increasing numbers of *P. nitidus* were correlated with a forward movement of *T. podicipina*, as shown by correlations with both the positions of posterior (r= -.398, df=26, P<.05) and medianth (r= -.324, df=26, .05<P<.10) individuals.

Other significant increases in overlap associated with increasing populations of helminths in *P. grisegena* were between a blood and tissue feeding nematode, *Capillaria obsignata* and a luminal dwelling cestode, *Wardium paraporale*, and between the small, intramucosal *Tatria biremis* and the large, lumen-mucosal *S. srivastavai*.

In *P. nigricollis*, no significant increases in overlap were seen. In *P. auritus, T. biremis* and *W. paraporale* had a significant increase. In *A. occidentalis*, however, the only case of increasing overlap was between two large, lumen dwelling absorbers, *W. paraporale*, and *Ligula intestinalis*. Both are residents in the posterior third of the intestine. *A. occidentalis* is the main host for both, but *W. paraporale* is a grebe specialist while *L. intestinalis* is a transient generalist with a short life span in the definitive host.

E. Discussion

Isolationist versus Interactive Communities

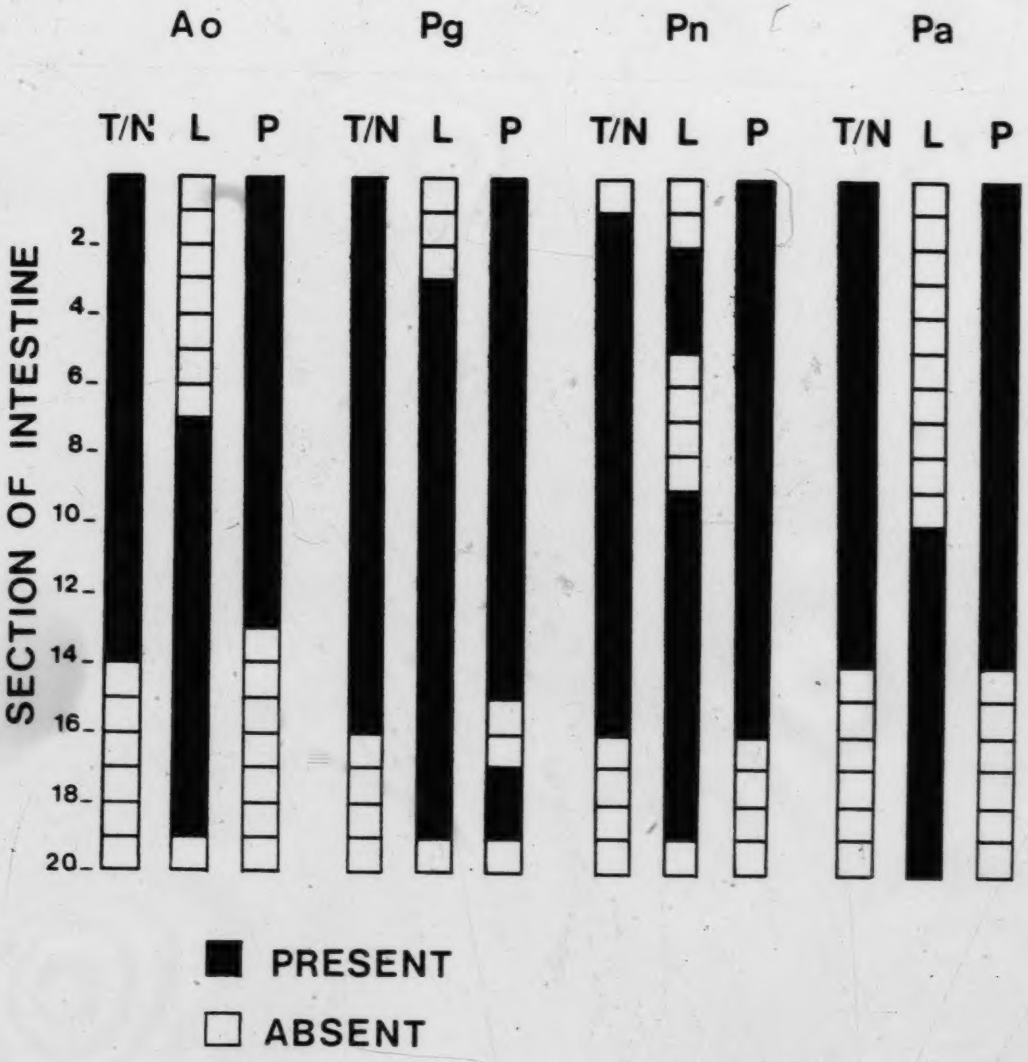
The intestinal helminth communities of grebes were generally large, species rich, and contained significant proportions of co-occurring species (see Chapter 2); all are characteristics of (and prerequisites for) interactive communities. In general, the patterns of resource exploitation, based on microhabitat distributions, supported the conclusion that these are interactive communities.

The fundamental niches of the common parasites in the intestines of grebes were generally broad, encompassing most of the intestine. Their realized niches, however, were small subsets of their fundamental niches, and when parasites occurred in more than one host species, they frequently occupied different positions. Nevertheless, the order of occurrence in relation to the other common species in each infracommunity was predictable. These features suggest that the degree of specialization of helminths to specific parts of the intestine does not limit them to a precise site, as assumed for isolationist communities; however, specialization may determine where they do best.

Several analyses provided direct evidence for interactive communities. Realized niches of adjacent species were arranged so as to markedly reduce the overlaps in their fundamental niches. Overlaps between species seldom increased when joint population size increased. Congeners that regularly co-occurred in the same infracommunities occupied complementary ranges. Finally, the distributions and abundances of some helminths in grebes, especially *Dioecocestus asper* and *Diorchis* sp. P, did affect those of other species. Interactions between helminths are important in determining the structure of infracommunities in grebes.

However, two of the analyses did not support the conclusion of interactive communities. The presence of many open sites (vacant niches) is generally considered to be a characteristic of isolationist, not interactive communities (Rohde, 1978; Price, 1984). Infracommunities in each of the grebe species included vacant sections, particularly toward the posterior end of the intestine. Vacant niches may be even more common. Intestinal parasites may be allocated to three different guilds on the basis of how and where they acquire nutrients (Bush, 1980; Bush and Holmes, MSb). Trematodes and nematodes (the engulfer guild) have intestinal tracts and typically engulf host tissues, sloughed epithelial material and luminal contents. Cestodes and acanthocephalans absorb nutrients through their body surfaces. Small absorbers are generally intimately associated with the hosts mucosal surface, the paramucosal zone, while larger absorbers frequently attach their scolices to the mucosal surface, but retain the bulk of their biomass in the lumen. Figure 19 shows the combined average distributions of the core species belonging to each of the three guilds in each host species. It is apparent that all grebes lack large, lumen-dwelling absorbers in the anterior intestine and small, paramucosal-dwelling absorbers and engulfers in the posterior intestine (*Capillaria obsignata* was considered a specialist of the caeca). The helminths of grebes do not appear to form saturated

Figure 19. The distribution of three guilds in the intestines of grebes. T/N = trematodes and nematodes (the engulfer guild), L = lumen dwellers, P = paramucosal dwellers. Ao = *Aechmophorus occidentalis*, Pg = *Podiceps grisegena*, Pn = *Podiceps nigricollis*, Pa = *Podiceps auritus*.


Ao
Pg
Pn
Pa
T/N
L
P
T/N
L
P
T/N
L
P
T/N
L
P
SECTION OF INTESTINE
2
4
6
8
10
12
14
16
18
20
■ PRESENT
☐ ABSENT

communities - vacant niches, indicative of isolationist communities, occur in most infracommunities and in the overall component communities.

In addition, in interactive communities, core species should be more evenly spread in niche space than would be expected by chance alone (Hanski, 1982; Bush and Holmes, MSb). However, broken-stick analysis indicated that none of the grebes had communities in which core species were significantly more evenly spread. This again suggests the presence of isolationist communities; however, it may also imply that the entire resource continuum is not equally available (the posterior terminal distances in *P. grisegena* infracommunities were frequently the largest).

Patterns of microhabitat distribution of helminths in lesser scaup (Bush and Holmes, MSb) are directly comparable to those observed in grebes. Bush and Holmes found that the fundamental niches of core species were large (over half the intestine) while realized niches were much smaller. Overlaps between species did not increase with increasing joint population size. Unlike the situation in grebes, core species in scaup were more evenly distributed than could be expected by chance alone. However, as in grebes, the community was not saturated (the trematode engulfer guild was frequently absent). Nevertheless, the core and secondary absorber species in scaup provided an interactive structure to the community. Therefore, the patterns of distribution of helminths in both scaup and grebes indicate that empty niches do not necessarily provide evidence for isolationist communities.

Butterworth (1982) identified a cline in the structure of communities of helminths in waterfowl ranging from those that were small, simple and unpredictable (isolationist communities, *e.g.*, *Anas americana*) to those that were large, complex and predictable (interactive communities, *e.g.*, *Melanitta fusca*). The communities in grebes were much more predictable than waterfowl communities with similar sizes and complexities (see Chapt. 2). Although interactions among helminths in grebes are important, they are not as pervasive as in the scaup system (Bush, 1980), possibly because of the smaller, simpler communities in grebes. Data in Pojmanska (1982) showed that interactions among three species of *Diorchis* in coots (*Fulica atra*) regulated the spatial distributions of these tapeworms when infrapopulations were high. When populations were low, the communities resembled isolationist assemblages.

The Importance of Adaptations

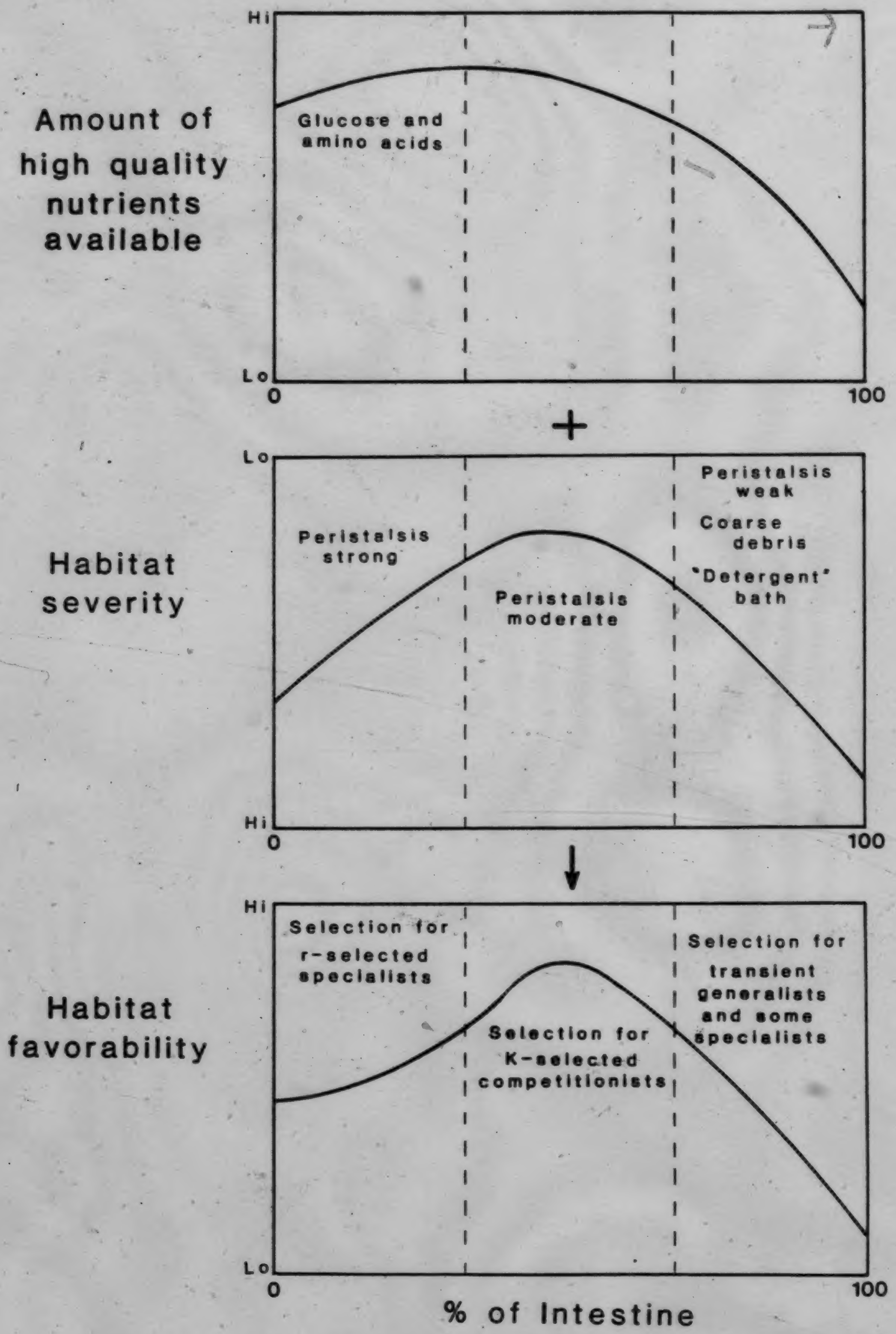
The theory of habitat selection suggests that organisms exist in areas within which their per capita fitness is optimal. Studies of the vertebrate intestine as a habitat for parasitic helminths, shows that it represents a complex environment that varies greatly in physical and chemical features along its length (see review by Crompton and Nesheim, 1976).

Because of the very different conditions that exist along the intestinal gradient, we might expect that different species of helminths in various regions of the small intestine have been molded by quite different selection pressures. Since the vertebrate small intestine has traditionally been considered as being composed of three histologically distinct regions, the duodenum, jejunum and ileum, and since the distribution of numbers of parasites of at least one species of grebe (*P. nigricollis*) demonstrated a similar trimodal pattern, the potential selective forces and adaptations of helminths in grebes will be considered under three broad categories, those in the anterior, mid and posterior intestines (Fig. 20).

Helminths in the proximal third of the intestine are subjected to pulsations of the villi, violent flow of ingesta, sigmoidal contractions, and the strongest peristalic waves in the alimentary canal (Crompton, 1970). Parasites in this region have at least two options: to avoid these forces by being small enough to hide among the well developed villi and complex folds of the mucosa, or to use extensively developed adaptations for attachment, or both.

Cestodes, which formed the majority of species in the grebe infracommunities, use the scolex as the main organ of attachment. The scolices of most of the cestodes of grebes have four muscular suckers and a retractable rostellum armed with hooks that differ in size and shape. (The exceptions are *Dioecocestus asper*, in which the rostellar hooks are

Figure 20. A model of differential selection pressures in three regions of the small intestine acting on absorber parasites.

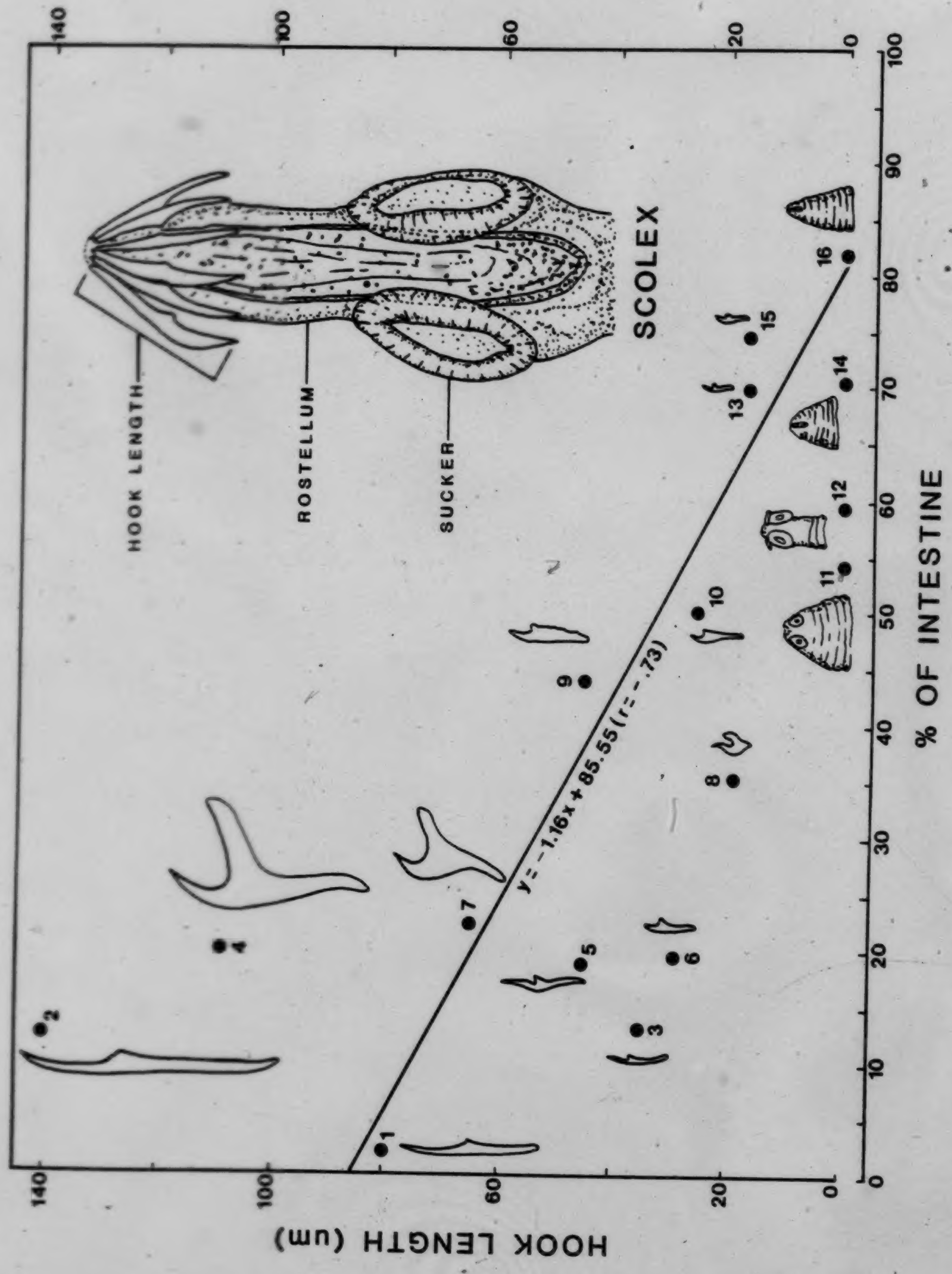

Amount of high quality nutrients available
Hi
Lo
0
100
Glucose and amino acids
+
Habitat severity
Lo
Hi
0
100
Peristalsis strong
Peristalsis moderate
Peristalsis weak
Coarse debris
"Detergent" bath
Habitat favorability
Hi
Lo
0
100
Selection for r-selected specialists
Selection for K-selected competitionists
Selection for transient generalists and some specialists
% of Intestine

lost as the worm matures in the definitive host, *Tetrabothrius immerinus*, which has suckers and muscular appendages but no hooks, and *Ligula intestinalis* and *Schistocephalus solidus*, which have two slit-like bothria, but no suckers or hooks).

For most species, simple rostellar hook length may be used as an index of attachment ability. Hook lengths of cestode specialists of grebes were negatively correlated with mean median position (Fig. 21). Those species in the anterior intestine had longer hooks than those in the posterior, suggesting that cestodes in the proximal intestine were specialized for their ability to attach and withstand peristaltic movements. Other features of cestodes in the anterior intestine related to maintaining their position include minute spines on the sucker surfaces (*e.g.*, *Tatria biremis*, *Schistotaenia* spp.), small wedge-shaped bodies (*e.g.*, *T. biremis*, *Pararetinometra lateralacantha*), and accessory sickle-shaped hooks on the posterolateral proglottid margins (*e.g.*, *P. lateralacantha*).

Reproductive structures may also reflect the attachment and flow problems encountered in the anterior intestine. Cestodes in the proximal intestine have well-developed structures for contacting mates and delivering sperm. The cirri (male intromittant organs) are armed with spines and are extremely long. In addition, accessory organs such as stylets may be present. Amabiliid tapeworms are known to use a hypodermic impregnation method to insert the cirrus

Figure 21. The correlation between cestode rostellar hook length, and mean median position in the intestine of the main host. 1 = Pararetinometra lateralacantha, 2 = Nadejdolepis sp. 3 = Diorchis sp. O, 4 = Schistotaenia colymba, 5 = Tatria biremis, 6 = Dubininolepis furcifera, 7 = Schistotaenia srivastavai, 8 = Tatria decacnatha, 9 = Dubininolepis podicipina, 10 = Diorchis sp. P, 11 = Dioecocestus asper, 12 = Tetrabothrius immerinus, 13 = Parafimbriaria websteri, 14 = Ligula intestinalis, 15 = Wardium paraporale, 16 = Schistocephalus solidus.


HOOK LENGTH (um)
% OF INTESTINE
0
10
20
30
40
50
60
70
80
90
100
140
100
60
20
0
y = -1.16x + 85.55 (r = -.73)
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
HOOK LENGTH
ROSTELLUM
SUCKER
SCOLEX

through the tegument and into the body of another worm. Specialized dorsal-ventral canals, and a seminal receptacle that interconnects all mature proglottids, may also be present. These specializations for coping with peristalsis and other intestinal movements appear to be very well developed in cestodes of grebes, which feed extensively on animal matter and have very muscular intestines (at least when compared to most waterfowl).

Other features of the proximal intestine are probably less deleterious. Cestodes are capable of using a variety of exogenous nutrients, including amino and fatty acids, but simple carbohydrates such as glucose and galactose are extremely important. Smyth (1969) pointed out that a shortage of carbohydrates resulted in stunting of growth, reduction in fecundity and production of abnormal eggs by *Hymenolepis diminuta* in rats. The anterior intestine has the highest secretory and absorptive activity. However, many complex sugars and proteins have not been completely broken down into more readily usable forms.

Although variable, the proximal intestine is generally more acidic than the distal intestine. Furthermore, metabolic wastes of cestodes using glucose include succinic and lactic acids that can contribute to luminal acidity (Mettrick, 1980). Studies of *H. diminuta* in rats showed that tapeworms concentrated their biomass, and migrated toward segments of the intestine with low pH. Interestingly, Mettrick and Podesta (1974) showed that decreased pH interfered with the host's ability to absorb glucose, thus providing a higher concentration of this nutrient in the paramucosal region.

Overall, the anterior intestine of grebes provides a nutrient rich site that is subjected to violent peristalsis. Helminths in this area were specialized for their ability to attach and reproduce in an agitated environment. Variance around mean median positions were smaller for these species than for species in the less perturbed mid and posterior intestinal segments. Helminth species richness and mean intensities of infection were higher and more predictable in the proximal third of the intestine.

The posterior third of the small intestine is a harsh environment for helminth parasites. Nutrients in the form of simple carbohydrates have been extracted by the host and are relatively scarce and unpredictable. *Diphyllobothrium* sp., a cestode, when collected from the posterior third of the intestine of a rat experimental host, had 25% higher protein content and less glycogen than those worms from the anterior two-thirds (Archer and Hopkins, 1958), which suggests that amino acids are more heavily used in relation to carbohydrates in the posterior intestine. Pancreatic and gastric secretions, mucous and sloughed intestinal epithelium are important sources of endogenous protein.

Bile and bile salts, released in the anterior intestine, are important chemical cues that stimulate excystation, evagination of scolices, and establishment of many enteric helminths (Smyth, 1969). Bile salts in the distal intestine are deconjugated and dehydroxylated into secondary bile acids by bacterial action. These molecules are detergents which reduce surface tension (Mettrick, 1980). Helminths in the posterior intestine are essentially living in a detergent bath with relatively low quantities or poorer quality food.

Peristalsis is weaker in the posterior intestine, leading to the accumulation of coarse, undigestible luminal debris, especially in grebes that feed on fish and large acquatic invertebrates. This region is subject to considerable abrasion, so that a constant sloughing of mucosal surface epithelium occurs (Smyth, 1969).

Helminths have at least two options available for existence in the distal intestine: to avoid its limitations by using stored nutrients and reducing their time in the definitive host, or by specialization. The pseudophyllidean cestodes, *L. intestinalis* and *S. solidus* use the first approach. These species undergo almost all of their growth as metacestodes (plerocercoids) in fish and are very large. As a result, incoming worms have few nutrient requirements in the definitive host, and are transitory, usually remaining no longer than about seven days. Maturation and reproduction of *L. intestinalis* and *S. solidus* is rapid (within 24 hours after ingestion by the definitive host) and depends largely on a high temperature. As a result, the host spectrum for these species is wide and includes many fish-eating homeotherms (see review by Dubinina, 1964). McCaig and Hopkins (1963) found that experimental infections of *S. solidus* established in very different sites in different hosts, ranging from 20% of the intestinal length in pigeons to 80% in domestic ducks. Both *S. solidus* and *L. intestinalis* were found in the posterior intestines of the larger, fish-eating grebes in natural infections, but in the mid-intestines of the smaller, mainly invertebrate-eating species. Both tapeworms may be opportunistic species that take advantage of open sites (or are forced to use them) including the unfavorable conditions of the distal intestine.

Other species show specialized adaptations for existing in this area. *Capillaria obsignata*, a nematode, generally avoids the distal small intestine by inhabiting the caeca. In large infections, however, worms invade the intestine. *C. obsignata* is a host blood and tissue feeder that burrows the elongated anterior end into the mucosa. Thus, *C. obsignata* does not rely on luminal food and attaches without using a holdfast (such as a sucker) that requires surface tension. In addition, the nematode cuticle is resilient to the abrasiveness of coarse luminal debris. Similarly, the acanthocephalan *Polymorphus marilis* has a tough epicuticular surface and attaches deeply into the intestinal wall using a densely armed, retractable proboscis.

Overall, the distal small intestine of grebes provides a relatively nutrient poor, harsh habitat for intestinal helminths. Helminths in this area were either specialists, or more frequently, opportunistic generalists. For all grebes, this part of the intestine had the lowest and most unpredictable species richness and abundance of parasites. It is not surprising that the proportion or number of vacant sections increased toward the ileo-caecal junction.

The middle third of the intestine represents a compromise of some conditions in the anterior and posterior parts, as well as offering the highest concentrations of quality nutrients (simple carbohydrates and amino acids). Absorptive activity is high. In comparison to the proximal intestine, peristalsis and rate of flow of chyme are reduced. Villi and intestinal folds are well developed. Therefore, I propose that the mid-intestine is a more favorable location for absorber helminths, particularly cestodes, than are the proximal or distal ends. As such, if space is a limiting factor, then interspecific interactions among helminths might be expected to be particularly significant for those in the mid-intestine. This pattern was noted for the infracommunities in *P. grisegena* and *P. nigricollis*.

In *P. grisegena*, the large cestode, *D. asper*, resides in the mid-intestine. *D. asper*, or the pathological changes it induces in the mucosa, markedly affects the species richness, distributions, and intensities of other helminths in the mid-intestine. As such, I believe that *D. asper* qualifies as a "keystone" species (Connell, 1975) in the helminth community of *P. grisegena*. *D. asper* has many of the attributes predicted for a K-selected organism (Southwood, 1976). Its population size is constant and its body size is large. Its generation time is probably long (*D. asper* has been reported from birds collected in winter off the coast of California by Linton (1925) suggesting that they may live for at least a complete year), especially in comparison to hymenolepidid cestodes of waterfowl that can have generation times in their definitive hosts as short as ten days (Hair, 1975). The intrinsic rate of increase of *D. asper* is probably small; few eggs are found in adult female worms. Southwood predicted that large size, long generation time, low reproductive rate and populations near carrying capacity would lead to habitat degradation. The mucosal damage induced by *D. asper* may be an example; if so, it also appears to be an effective mechanism of interference competition. The totally dioecious reproductive condition of the Dioecocestidae may be another factor promoting competitive interactions. Esch *et al.* (1977) pointed out that hermaphroditism, monoeciousness, and protandrous hermaphroditism, "normal" cestode reproductive modes, not only confer the advantage of guaranteeing a mating partner, but also reduce the requirements for space and nutrient resources, thereby reducing competitive interactions.

Other grebes did not have a helminth species in the mid-intestine as distinctively and clearly superior as a competitor as was *D. asper* in *P. grisegena*. *Diorchis* sp. P, in *P. nigricollis*, resides in the mid-intestine and is associated with posterior shifts in the positions of two species (*Wardium paraporale* and *Tatria decacantha*) that occur behind it, but no noticable effects on species anterior to it. Neither *W. paraporale* or *T. decacantha* have *P. nigricollis* as a main host. In its main host, *A. occidentalis*, *W. paraporale* establishes in the mid-intestine and achieves a larger size than when present in other grebes (see Podesta and Holmes, 1970 and Gallimore, 1964), but negative interactions with other species could not be demonstrated.

Holmes and Price (1985) predicted the occurrence of two types of parasite communities: assemblages of micro-habitat specialists, with little or no interactions occurring in non-equilibrium, unsaturated communities; and assemblages of species with high density populations in equilibrium communities in which interactions are significant. Neither hypothesis alone adequately describes the infracommunities in grebes. Grebes have unsaturated communities in which interactions do occur, but are less significant than those noted in *Aythya affinis* (Bush, 1980; Bush and Holmes, MS). This may be due to the degree of adaptations necessary for the relatively unfavorable sections of the intestine in grebes. Infracommunities of intestinal helminths in grebes are composed of some micro-habitat specialized, relatively r-selected species (particularly in the anterior intestine); some K-selected competitionists (in the favorable mid-intestine); and some opportunistic generalists (and a few specialists) in the unfavorable posterior intestine. Although interactions that affect the distributions of some species certainly occur, they are by no means the sole force involved in determining community structure. Differential selection pressures exerted by the environment are also important.

Another factor that may be important in explaining the patterns of habitat use by helminths, is their evolutionary history. Complementary use of micro-habitat, and specialization by differential infection of different host species, were both noted for congeneric helminths. Investigation of host evolutionary history, in conjunction with that of host-specialized helminths will further elucidate these patterns.

F. Literature Cited

Archer, D.M., and C.A. Hopkins. 1958. Studies on cestode metabolism. V. The chemical composition of *Diphyllobothrium* sp., in the plerocercoid and adult stages. Exptl. Parasit. 7:542-554.

Bush, A.O. 1980. Faunal similarity and infracommunity structure in the helminths of lesser scaup. Ph. D. thesis. Univ. of Alberta, Edmonton. 254 pp.

Bush, A.O., and J.C. Holmes. 1983. Niche separation and the broken-stick model: use with multiple assemblages. Am. Nat. 122:849-855.

Bush, A.O., and J.C. Holmes. MSb. Intestinal helminths of lesser scaup ducks: An interactive community. Submitted to Can. J. Zool. 1985.

Butterworth, E.W. 1982. A study of the structure and organization of intestinal helminth communities in ten species of waterfowl (Anatinae). Ph. D. thesis. Univ. of Alberta, Edmonton. 217 pp.

Brown, J.H. 1975. Geographical ecology of desert rodents. pp. 315-341. In M.L. Cody and J.M. Diamond (eds.) Ecology and Evolution of Communities. Belknap Press, Cambridge, Mass. 543 pp.

Connell, J.H. 1975. Some mechanisms producing structure in natural communities: A model and evidence from field experiments. pp. 460-490. In M.L. Cody and J.M. Diamond (eds.) Ecology and Evolution of Communities. Belknap Press, Cambridge, Mass. 543 pp.

Crompton, D.W.T. 1970. An Ecological Approach to Acanthocephalan Physiology. Cambridge Univ. Press, Cambridge. 125 pp.

Crompton, D.W.T. 1973. The sites occupied by some parasitic helminths in the alimentary tract of vertebrates. Biol. Rev. 48:27-83.

Crompton, D.W.T., and M.C. Nesheim. 1976. Host-parasite relationships in the alimentary tract of domestic birds. Advances in Parasitology 14:95-194.

Dubinina, M.N. 1964. Cestodes of the family Ligulidae and their taxonomy. pp. 173-186 In R. Ergens and B. Rysavy (eds.), Parasitic Worms and Aquatic Conditions, Symposium, Oct. 29 - Nov. 2, 1962. Publ. Czech. Acad. Sci. 1964. 265 pp.

Esch, G.W., T.C. Hazen, and J.M. Aho. 1977. Parasitism and r- and K-selection. pp. 9-62. In G.W. Esch, (ed.), Regulation of Parasite Populations. Academic Press. New York. 253 pp.

Gallimore, J.R. 1964. Taxonomy and ecology of helminths in grebes in Alberta. M. Sc. thesis. Univ. of Alberta, Edmonton. 167 pp.

Hair, J.D. 1975. The structure of the intestinal helminth communities of lesser scaup (*Aythya affinis*). Ph. D. thesis. Univ. of Alberta, Edmonton. 92 pp.

Hanski, I. 1982. Dynamics of regional distribution: The core and satellite species hypothesis. Oikos 38:210-221.

Holmes, J.C. 1973. Site selection by parasitic helminths: Interspecific interactions, site segregation, and their importance to the development of helminth communities. Can. J. Zool. 51:333-347.

Holmes, J.C., and P.W. Price. 1985. Communities of parasites. Chapt. 9 In D.J. Anderson and J. Kikkawa (eds.), Community Ecology: Pattern and Process. Blackwell Sci. Co., Oxford.

Hurlbert, S.H. 1978. The measurement of niche overlap and some relatives. Ecology 59:67-77.

Hutchinson, G.E. 1957. Concluding remarks. Cold Spring Harbour Symp. Quant. Biol. 22:415-427.

Linton, E. 1925. A new diecian(sic) cestode. J. Parasitol. 11:163-169.

MacArthur, R.H. 1957. On the relative abundance of bird species. Proc. Natl. Acad. Sci. USA. 43:293-295.

McCaig, M.L.O., and C.A. Hopkins. 1963. Studies on *Schistocephalus solidus*. II. Establishment and longevity in the definitive host. Exptl. Parasit. 13:273-283.

Mettrick, D.F. 1980. The intestine as an environment for *Hymenolepis diminuta*. pp. 281-356 In H.P. Arai (ed.), Biology of the Tapeworm *Hymenolepis diminuta*. Academic Press. New York. 733 pp.

Mettrick, D.F., and R.B. Podesta. 1974. Ecological and physiological aspects of helminth-host interactions in the mammalian gastrointestinal canal. Advances in Parasitology 12:183-278.

Podesta, R.B., and J.C. Holmes. 1970. Hymenolepid cysticercoids in *Hyallela azteca* of Cooking Lake, Alberta: Life cycles and descriptions of four new species. J. Parasitol. 56:1124-1134.

Pojmanska, T. 1982. The co-occurrence of three species of *Diorchis* Clerc, 1903 (Cestoda: Hymenolepididae) in the European coot, *Fulica atra* L. Parasitol. 84:419-429.

Price, P.W. 1980. The Evolutionary Biology of Parasites. Princeton Univ. Press, Princeton, N.J. 237 pp.

Price, P.W. 1984. Communities of specialists: Vacant niches in ecological and evolutionary time. pp. 510-523 In D.R. Strong, Jr., D. Simberloff, L.G. Abele and A.B. Thistle (eds.), Ecological Communities: Conceptual Issues and the Evidence. Princeton Univ. Press, Princeton, N.J. 613 pp.

Pianka, E.R. 1975. Niche relations of desert lizards. pp. 292-314 In M.L. Cody and J.M. Diamond (eds.), Ecology and Evolution of Communities. Belknap Press, Cambridge, Mass. 543 pp.

Rohde, K. 1978. Latitudinal differences in host specificity on marine Monogenea and Digenea. Mar. Biol. 47:125-134.

Smyth, J.D. 1969. The Physiology of Cestodes. W.H. Freeman and Co., San Francisco. 279 pp.

Southwood, T.R.E. 1976. Bionomic strategies and population parameters. pp. 26-48 In R.M. May (ed.), Theoretical Ecology. Blackwell Sci. Publ. London. 317 pp.

Tolkacheva, L.M. 1983. Dioecious cestodes. (in Russian, English summary) Parazitologiya 17:427-429.

IV. General Discussion: Coevolutionary Constraints on Community Structure

A. Introduction

Any study of community organization can be refined by considering the evolutionary affinities of the species in that community (Brooks, 1980). Studying communities in an historical context adds a three-dimensional perspective lacking in a static ecological study. The broad field of coevolution marries ecology and evolution because it considers the conditions under which reciprocal genetic responses between species may be seen. Roughgarden (1983) defined coevolution as "...the simultaneous evolution of ecologically interacting populations." Roughgarden pointed out that, for coevolutionary constraints to apply to a system, the populations in that system must interact or have interacted in the past, and must have been together long enough for the interaction to have had a realistic opportunity to cause evolutionary changes.

Symbiotic systems, particularly parasitic ones, have been considered to be among the most likely to provide evidence of coevolution. Coevolution between hosts and parasites has been suggested for a long time (see review in Holmes, 1983), and has led to the formulation of several "rules" (Mitter and Brooks, 1983). Among these are Fahrenholz's rule, which claims that parasite phylogeny mirrors that of the host, and Manter's rule, that long association between hosts and parasites leads to tight host specificity.

Many studies have explored the validity of these rules, but few have considered the potential for coevolution among parasites within a community. Rohde (1979) and Price (1980, 1984) proposed that coevolution between parasites was insignificant, while that between host and parasite was substantial; parasite communities were regarded as young assemblages of species adaptively specialized to exploit specific microhabitats in patchily distributed hosts. In contrast, Holmes (1973, 1983) suggested that parasite communities were old, and that regular interactions between parasites had led to coevolution, resulting in niche segregation (selective site segregation). Coevolution between parasites was also assumed for cases in which site segregation was presumed to minimize hybridization (Sogandares-Bernal, 1959; Martin, 1969). The differences in opinion as to how much the functional relationships between parasites in a community were shaped by coevolution resided in their disagreements about how well parasitic systems met the criteria for coevolution, as stated by Roughgarden (1983). Holmes and Price (1980, 1985) attempted to unify these views by postulating different degrees of coevolution between parasites in interactive and isolationist communities.

The relevance of considering coevolution to interpret an ecological pattern was demonstrated in Holmes and Price

(1980). Holmes (1971) described habitat segregation of two blood flukes, *Aporocotyle macfarlani* and *Psettarium sebastodorum*, in scorpaenid rockfishes. The flukes had different dominant hosts and also differed in their depth preferences; *A. macfarlani* was associated with shallow reefs, *P. sebastodorum* had a wide depth range. The flukes also differed in microhabitat distribution. *A. macfarlani* occurred in the lumen of the afferent branchial arteries, the ventral aorta, and rarely in parts of the heart. *P. sebastodorum* occurred mainly in the heart. Overlap in the distributions of the two flukes was reduced in concurrent infections. Therefore, the evidence of resource partitioning by the trematodes suggested selective site segregation, indicative of coevolution. Analysis of phylogenies of hosts and parasites, however, showed that the relationship between *P. sebastodorum* and *A. macfarlani* was not ancient, in that the genealogies of the parasites and hosts were not congruent. Holmes and Price suggested that for both species of parasite, their presence in rockfish was an example of "host capture" or a colonization event. Moreover, they suggested that the current distributions of *A. macfarlani* and *P. sebastodorum* resulted primarily from invasion by species preadapted to different sites, with the influence of long term competition (if important at all), limited to reducing *A. macfarlani* infections in the bulbus arteriosus. In this case, the evidence supports Price's interpretation of parasite communities as being relatively recent assemblages of microhabitat specialists.

Holmes and Price (1980) also pointed out, however, that parasite communities were unlikely to coevolve as whole units. In order for the potential of coevolution to be significant, parasite species have to (or had to) co-occur regularly. If Hanski's (1982) core/satellite model adequately describes parasite communities, then signs of coevolution would be expected predominently among core species (or recurrent group species in the terminology of Fager, 1957; Fager and McGowan, 1963). Satellite species would have little opportunity to coevolve.

The object of core/satellite or recurrent group analysis is to identify naturally occurring groups that consistently and frequently are found together within any assemblage of species. As pointed out in Chapter 2, the intestinal helminths in *A. occidentalis*, *P. grisegena* and *P. nigricollis* had bimodal frequency distributions, each with a group of core and recurrent group species. These core or recurrent group members were responsible for most of the similarity within each community in each host. The identities and relative abundances of core species for each grebe, resulted in characteristic and predictable communities.

Hanski (1982) predicted that core species would be biologically accommodated and more evenly distributed in niche space than the inconstant and unpredictable satellite species. Evaluation of microhabitat segregation and patterns of overlap among core species in grebes (Chapt. 3) showed that interspecific interaction among them was a significant factor in grebe infracommunities. Therefore, core species units appear to meet the criteria of Roughgarden (1983), and signs of coevolution should be evaluated among these species.

Evidence for coevolution among some core species of grebes is hard to evaluate. The family Hymenolepididae encompasses a large group of questionably related genera. The genus *Diorchis* includes many species (at least 30 according to Spasskaija, 1966), that infect a wide variety of birds. Only two species, both of which require further taxonomic study, have been reported from grebes. This limited diversity prevents a comprehensive coevolutionary analysis. The genus *Dubininolepis* (=*Confluaria* in Spasskaija, 1966) has 9 species and includes worms that are host specific to grebes. Unfortunately, taxonomic confusion, possible morphological variation with worm age (ontogenetic differences, Korpaczewska, 1960) and probable misidentifications precludes any phylogenetic analysis based on records or descriptions in the literature. Therefore, examination of the important hymenolepidid core species in grebes for signs of coevolution, is currently not feasible.

Similarly, the other core species suffer from either taxonomic confusion, or an insufficient knowledge of their diversity in grebes. The Dioecocestidae includes 7 species, 6 of which are strictly specific to grebes. Unfortunately, some species descriptions are based on the presence or absence of rostellar hooks - a feature that is known to be dependant on the age of the individual parasite (Jogis, 1978). Jogis concluded that all dioecocestids described from holarctic grebes were likely to be a single species, *D. asper*. Therefore, although this group of tapeworms shows strict host specificity, the number of species in the group is uncertain.

Congeneric species of intestinal helminths in grebes demonstrated site segregation, differential abundances in different host species, and host specificity (see Chapt. 2). Two of the four sets of congeners in grebes (*Tatria biremis* and *T. decacantha; Schistotaenia colymba, S. srivastavai and S. tenuicirrus*) are members of the same family, Amabiliidae. The amabiliids (with one exception to be discussed later) are host specific to grebes. Within the communities examined, the members of this family alone represented 29% of the core species (27% of the recurrent group species). These amabiliids appear to meet Roughgarden's qualifications for species that may demonstrate coevolutionary attributes: they are host specific and frequently co-occur, suggesting a long and recurrent association, and they demonstrate niche differentiation suggesting interaction.

The amabiliids represent a group that has been recovered on five continents from three genera of grebes. Furthermore, the group has been subject to at least three taxonomic reviews (Korpaczewska and Sulgostowska, 1974;

Ryzhikov and Tolkacheva, 1975, 1977). Because this group includes a significant proportion of the core species found in the hosts examined, and since they are relatively better known than other parasites of grebes, the amabiliids will be examined for evidence of coevolution with their hosts.

B. Host Phylogeny

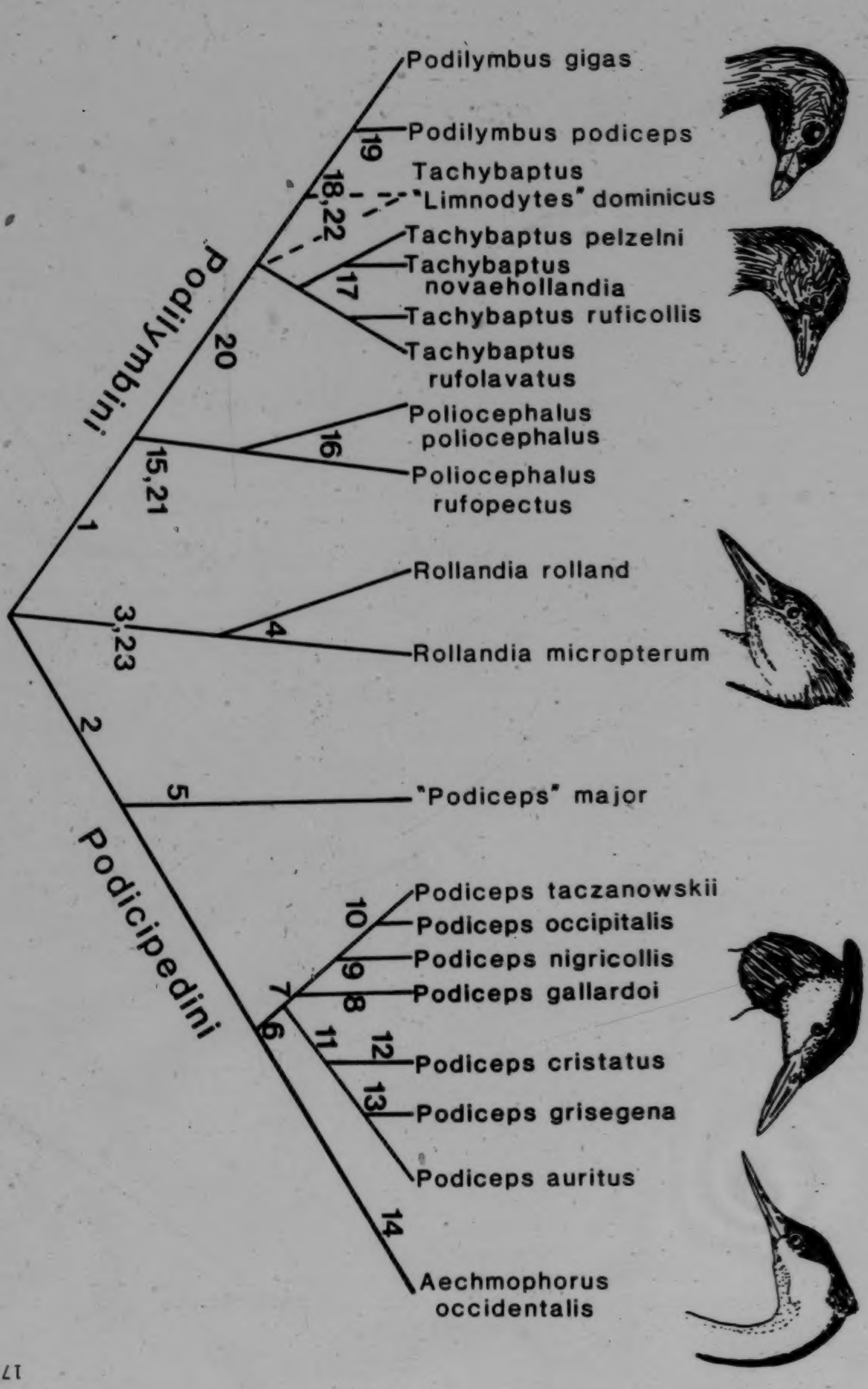
The family Podicipedidae comprises 20 extant species in seven genera, distributed worldwide (Cramp and Simmons, 1977) (Table 1). Undoubtedly, grebes are an ancient group of birds (Storer, 1963a; Cracraft, 1982). Fossils, ascribable to the extant genera *Podiceps* and *Podilymbus*, are known from the Miocene (20 million years before the present) from North America (Feduccia, 1980). Thus, grebes have existed, essentially unchanged, for a long time.

The phylogenetic scheme for grebes presented in Figure 1 has not been derived from cladistic analysis and thus is not a true cladogram, although it is presented in that form. It is based on data on the elaborate courtship behaviors, vocalizations, patterns of downy young, and morphological characteristics of grebes documented in a series of papers by R.W. Storer (1961, 1963a, 1963b, 1967a, 1967b, 1971, 1976) and K.E.L. Simmons (1954, 1968, 1974). Storer frequently made assessments of the evolutionary affinities of grebes, and the scheme presented here is a compilation and integration of his ideas. The rationale for the host phylogeny follows (numbers in parentheses correspond to

Table 1. The distribution of grebes of the world.

Species	Distribution
Podilymbini	
Tachybaptus ruficollis	Palearctic, Africa, South-east Asia
T. novaehollandiae	Australia, South-east Asia
T. pelzelni	Madagascar
T. rufolavatus	Madagascar
T. dominicus	South America, North America
Podilymbus podiceps	South America, North America
P. gigas	Guatemala
Poliocephalus poliocephalus	Australia
P. rufopectus	New Zealand
Rollandia rolland	South America
R. micropterum	South America
Podicipedini	
"*Podiceps*" *major*	South America
Podiceps auritus	Holarctic
P. cristatus	Palearctic, Africa, Australia, New Zealand
P. gallardoi	South America
P. grisegena	Holarctic
P. nigricollis	Holarctic, South America, Africa
P. occipitalis	South America
P. taczanowskii	South America
Aechmophorus occidentalis	Nearctic

Figure 1. A phylogenetic scheme for the Podicipedidae. See text for characters represented by numbers at branch points.


Podilymbini
Podicipedini
Podilymbus gigas
Podilymbus podiceps
Tachybaptus "Limnodytes" dominicus
Tachybaptus pelzelni
Tachybaptus novaehollandia
Tachybaptus ruficollis
Tachybaptus rufolavatus
Poliocephalus poliocephalus
Poliocephalus rufopectus
Rollandia rolland
Rollandia micropterum
"Podiceps" major
Podiceps taczanowskii
Podiceps occipitalis
Podiceps nigricollis
Podiceps gallardoi
Podiceps cristatus
Podiceps grisegena
Podiceps auritus
Aechmophorus occidentalis
1
2
3,23
4
5
6
7
8
9
10
11
12
13
14
15,21
16
17
18,22
19
20

those at the branch points in the phylogenetic scheme, Fig. 1).

Grebes can be divided into two well-differentiated tribes, the Podicipedini and Podilymbini, plus an intermediate genus, *Rollandia*, on the basis of differences in courtship and copulatory behavior. The Podilymbini do not have elaborate courtship displays, but do use vocalizations extensively. During copulation, there is stroking of the breast of the "active" bird. In addition, all have a well-developed *flexor perforatus digiti II* muscle with a separate canal through the hypotarsus for the tendon of insertion (Storer, 1963a) (1). The tribe Podicipedini all have elaborate courtship displays, often involving erectile plumes on the sides and tops of the head. During copulation, there is no stroking of the active bird. The extra canal in the hypotarsus is absent (2).

The genus *Rollandia* seems intermediate, sharing some features with both the Podicipedini and Podilymbini, and having some characteristics that are unique. Like the Podilymbini, *Rollandia* spp. have a well developed *M. flexor perforatus digiti II* with a separate canal in the hypotarsus, although the canal is smaller and in a slightly different location (3) (Storer, 1967b). Like the Podicipedini, *Rollandia* spp. have head plumes used in courtship displays and do not stroke the active bird during copulation (23). Unlike either tribe, *Rollandia* spp. have an iridescent plumage, a unique "bumping" ceremony, and downy young unlike those of any other grebes, lacking both bare crown spots or rufous head patches (4) (Storer, 1967a).

The position of *"Podiceps" major* is contentious. Storer (1963b) showed that the copulatory behavior and lack of the extra canal in the hypotarsus placed it in the Podicipedini, but that major differences in courtship behavior (*e.g.*, lack of a "discovery" ceremony and a "cat" display) suggested that it was not close to other *Podiceps* spp. Downy young of *P. major*, have a bare crown patch (like other *Podiceps* and *Aechmophorus*) but unlike *Aechmophorus*, the young are striped. The pattern of striping is very different from *Podiceps sensu stricto*, however, in that a "bull's eye" pattern occurs on the head and there are seven, rather than nine stripes on the body (Storer, 1967a). Originally, *P. major* was placed in the genus *Aechmophorus*; however, Wetmore and Parks (1954) showed that in form and feeding habits, despite a superficial resemblance to *Aechmophorus occidentalis*, the structure of the cervical and thoracic vertebrae were different. Storer (1963b) concluded that *P. major's* resemblance in form to *Aechmophorus*, and in color pattern to *Podiceps grisegena*, were the results of convergence, and that *"Podiceps" major* probably deserved generic rank. Because it resembles *Rollandia* by having an iridescent back, it has been placed near the origin of the Podicipedini (5).

The core of the tribe Podicipedini is formed by seven species assigned to the genus *Podiceps*. All have striped downy young with bare crown patches and all perform a characteristic "discovery" ceremony during courtship (6) (Storer, 1963a, 1967a). Within this group, four species are small and gregarious; all have post-orbital plumes, courtship without "weed" ceremonies, and young that lack a central white stripe or spot behind the crown spot (7). Within this group, *P. gallardoi* has the simplest downy young head pattern (8). Young of *P. occipitalis* and *P. nigricollis* are unique in having two white stripes on each side of the crown. This, and behavioral similarities, led Storer (1967a) to conclude that *P. occipitalis* is a geographical and ecological representative of *P. nigricollis* (9). *P. taczanowskii*, however, is sympatric with *P. occipitalis* and feeds on fish rather than small invertebrates. Storer concluded that *taczanowskii* was a "recent offshoot" of *occipitalis* because of the morphological similarities in downy young, as well as the fact that both have "barging" and "diving" displays (10).

The larger species of *Podiceps* all have "weed" ceremonies, and all use the same posture while sunbathing (11). The posture of *P. cristatus* at the climax of the "discovery" ceremony, and the "ripple" dive of that species are unique among *Podiceps* (12) (Simmons, 1974). *P. grisegena* and *P. auritus* do not use wing-spreading in the "cat" display; both use a "penguin" dance at the climax of the "discovery" ceremony; both use "bouncy" dives as display dives; and their vocalizations are very similar (13)

(Storer, 1967a).

Aechmophorus occidentalis has a "penguin" dance with weeds that resembles that of *P. grisegena* and *P. cristatus*; however, the famous "rushing" ceremony, courtship feeding, and neck posturing are different (14) (Storer, 1963a). In addition, the thoracic vertebrae of *A. occidentalis* are unique among grebes (Wetmore and Parkes, 1954). As for *P. major* and the other Podiceps spp., downy young of *Aechmophorus* have a bare crown patch. However, a unique characteristic of *Aechmophorus* is the obliteration of any striping.

Within the tribe Podilymbini, two species in the genus *Poliocephalus* occur in the Australian region. Although displaying many morphological characteristics of the true dabchicks (*Tachybaptus* and *Podilymbus*), *Poliocephalus* spp. are behaviorally different. The head of the passive bird is not raised to stroke the breast of the active bird during copulation, as is noted for *Tachybaptus* and *Podilymbus*, and *Poliocephalus* spp. have a unique "patter" ceremony. Fewer and softer vocalizations than the dabchicks are used during courtship (15) (Storer, 1971). As for all Podilymbini, the young have rufous down on the crown of the head. *Poliocephalus rufopectus* has a "diving" ceremony that is very similar to the exceptional "bumping" ceremony of *Rollandia* spp., but no contact between mates occurs. Storer (1971) concluded that *Poliocephalus*, although in the tribe Podilymbini, had no close relatives (21). *P. rufopectus* in

New Zealand is a geographic representative of *P. poliocephalus* of Australia (16).

The other Podilymbini have "diving" and "pattering" displays that differ markedly from *Poliocephalus* (20). Both *Tachybaptus* and *Podilymbus* use many strident vocalizations, including trills.

The genus *Tachybaptus* includes five species, all of which have downy young with rufous stripes on the back (Storer, 1967a). The position of the New World species, *T. dominicus*, is somewhat uncertain. Although previously placed in the genus *Podiceps*, morphological and behavioral evidence (*e.g.*, rufous on downy young, use of vocalizations) clearly place it in the tribe Podilymbini. The downy young of *T. dominicus* have rufous patches but differ from *T. ruficollis* in details of striping. Storer (pers. comm.) would place *dominicus* in *Tachybaptus* (22); Simmons suggested that differences between *T. dominicus* and other species in the genus warranted a separate genus, *Limnodytes* (18).

The remaining four species in *Tachybaptus* are from the Old World. Two, *T. pelzelni* and *T. rufolavatus*, occur on Madagascar. Voous and Payne (1965) considered *T. pelzelni* to be the "oldest" species on Madagascar due to its unique plumage and coloration. *T. rufolavatus* and *T. ruficollis* are similar in plumage, can and do interbreed, and were considered conspecific by Voous and Payne (1965). Little information is available on morphology or behavior of the East Indian species, *T. novaehollandiae*. Storer (1967a) pointed out differences in the patterns of downy young among the Old World *Tachybaptus* species, but considered them to be closely related. *T. ruficollis* and *T. novaehollandiae* have a patch of long, silvery white hairlike down on the forehead, however, *T. novaehollandiae* and *T. pelzelni* differ from *T. ruficollis* in having pure white stripes on the back and white on the face, throat and crown of the downy young (Storer, 1967a). Therefore, other than the distinctive position of *T. dominicus*, the pattern of relationships among the species of *Tachybaptus* are questionable (17).

Podilymbus seems to be an offshoot of *Tachybaptus*-like grebes, modified for eating crayfish and molluscs. The ulnar origin of *M. extensor longus digiti II* is not confined to the extreme proximal end of the bone and the distal head of *M. extensor longus digiti III* is absent (Sanders, 1967). The bill is short, deep and powerful, and strongly pied in the breeding season. Feathers of the lores, forehead and malar region have broad, flattened tips to the rachis (Stettenheim, 1974). Pied-billed grebes have a sexually dimorphic "song" and a unique "pivoting" display. These features isolate them from the other Podilymbini (19). The flightless Atitlan grebe of Guatemala, *P. gigas*, is probably a geographic form of *P. podiceps*.

Therefore, the phylogenetic scheme proposed for the Podicipedidae shows three main branches: the tribes Podicipedini and Podilymbini, and the genus *Rollandia*.

C. Zoogeography of Grebes

Grebes represent one of the oldest of the bird groups. Fossils are known from the Oligocene (*Podiceps*), Pliocene (*Aechmophorus, Pliodytes, Podiceps*), and Pleistocene (*Podiceps, Aechmophorus, Podilymbus*) (Palmer, 1962; Murray, 1967). Rich (1983) stated that five genera of grebes (identities not specified) are known from the mid to late Cretaceous (about 100 to 80 million years before the present, MYBP). At this time, Gondwanaland was breaking up (Brown and Gibson, 1983). By the end of the Cretaceous (about 65 MYBP), the gap between Brasil and west Africa was more than 800 km of open ocean (Brown and Gibson, 1983). Cracraft (1973) cited evidence for a landbridge between Brasil and west Africa up to 94 MYBP. South America and Antarctica were connected until the Mesozoic (150 MYBP). New Zealand was attached to Antarctica, but broke away around 80 MYBP.

Madagascar and India broke away from Gondwanaland so that by 80 MYBP the Mozambique Channel had formed. Madagascar was believed to have separated at or before 100 MYBP, and was separated from the Indian subcontinent by 80 to 90 MYBP. However, interpretation of the geology of the Indian Ocean basin is controversial, and India, Africa and Madagascar may not have separated from each other until the late Cretaceous (75 MYBP) (Cracraft, 1973).

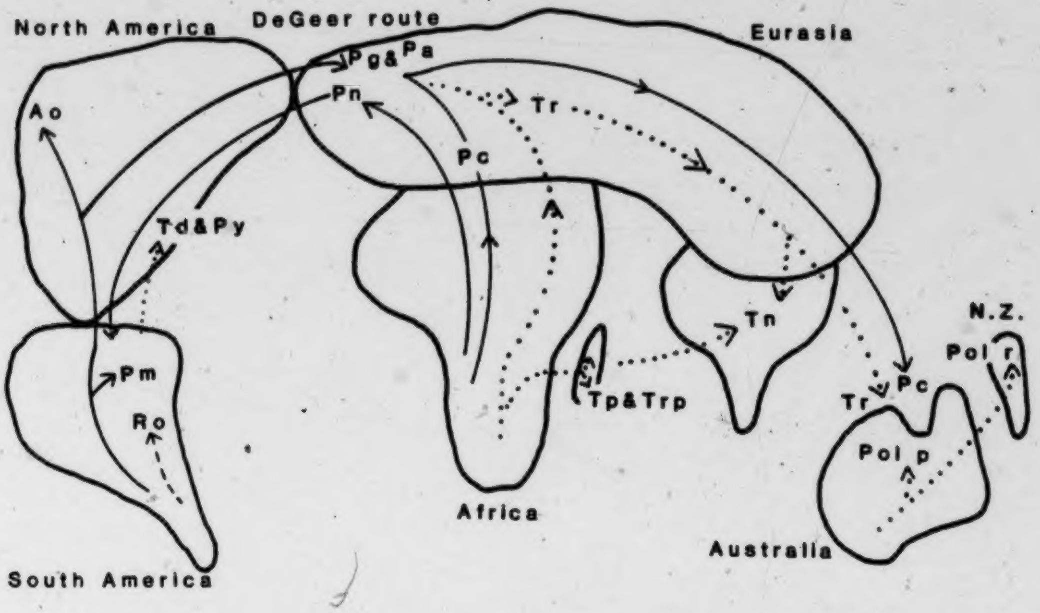
In Laurasia, land connections between North America and northeastern Europe persisted until the lower Eocene (about

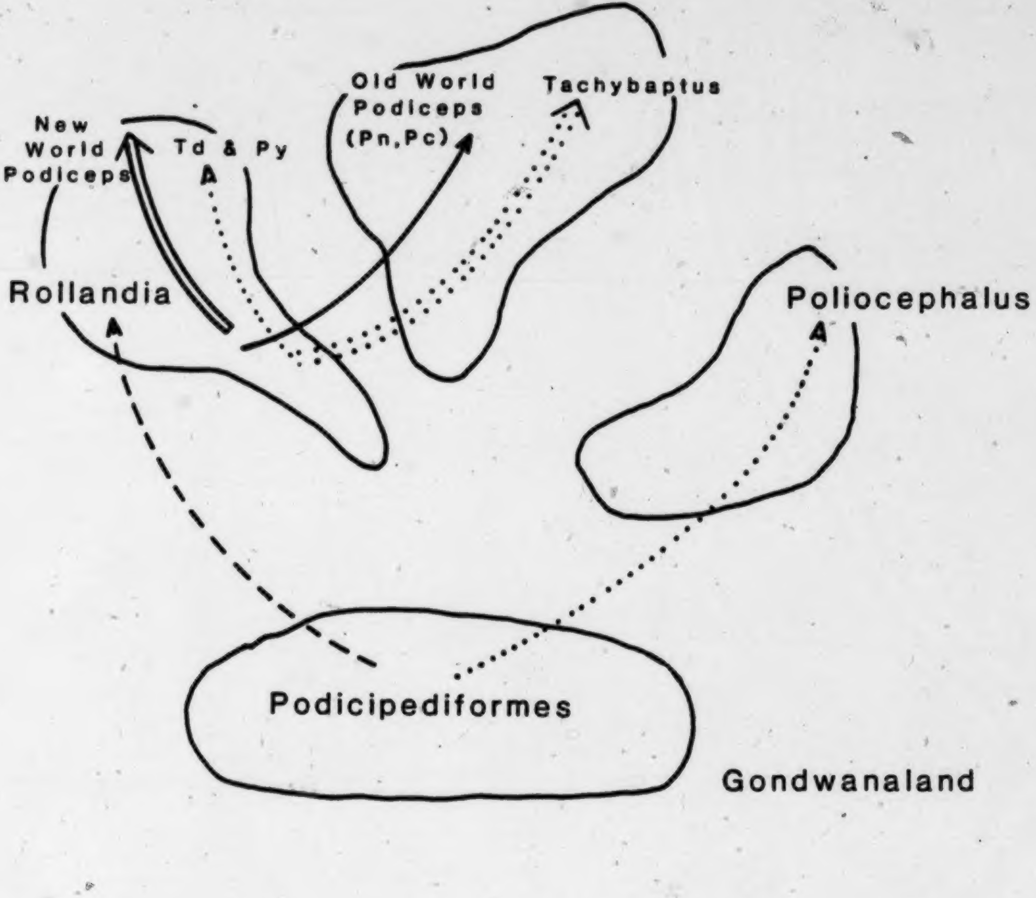
60 MYBP). This northern connection has been called the De Geer Route, and probably presented an important corridor for the migration of animals between the Old and New Worlds (Brown and Gibson, 1983).

Africa is thought to have collided with Asia through Arabia in the mid Tertiary (about 40 MYBP). Events during the Cretaceaous are uncertain in Central America, but it is generally believed that a land bridge between Mexico and South America existed up to the lower Cretaceous (about 135 million years BP).

Based on the geological history, the presumed age of grebes, and the phylogenetic scheme outlined above, a zoogeographic model of the group can be advanced (Fig. 2). Storer (1967b) suggested that the presence in South America of *Rollandia*, the "primitive" *"Podiceps" major*, and the fact that South America has the most diversified grebe fauna of any continent could be used as arguments that the family originated there (Storer, 1967b). Assuming a South American origin of the Podilymbini in the early to mid Cretaceous, the ancestral *Poliocephalus* line presumably reached the Australian-New Zealand area (from Antarctica) and differentiated there before the true dabchicks (*Tachybaptus*) and *Podiceps cristatus* arrived. Therefore, *Poliocephalus poliocephalus* and *P. rufopectus* would have been isolated from their relatives for a long time (Storer, 1971). The remaining stocks of the Podilymbini were split. As Africa-Madagascar-India moved away from Gondwanaland, the

Figure 2. A zoogeographic model for the distribution of grebes. Ao = *Aechmophorus occidentalis*, Pa = *Podiceps auritus*, Pc = *Podiceps cristatus*, Pg = *Podiceps grisegena*, Pm = "*Podiceps*" *major*, Pn = *Podiceps nigricollis*, Pol p = *Poliocephalus poliocephalus*, Pol r = *Poliocephalus rufopectus*, Py = *Podilymbus podiceps*, Ro = *Rollandia rolland*, Td = *Tachybaptus dominicus*, Tn = *Tachybaptus novae-hollandiae*, Tp = *Tachybaptus pelzelni*, Tr = *Tachybaptus ruficollis*, Trp = *Tachybaptus rufolavatus*. N.Z. = New Zealand.


North America
DeGeer route
Eurasia
Pg&Pa
Pn
Tr
Ao
Pc
Td&Py
Tn
N.Z.
Pol r
Pm
Tp&Trp
Tr
Pc
Ro
Pol p
Africa
Australia
South America


Old World
Podiceps
(Pn,Pc)
Tachybaptus
New
World
Podiceps
Td & Py
Rollandia
Poliocephalus
Podicipediformes
Gondwanaland

Tachybaptus ancestral stock (other than the ancestor of *T. dominicus = Limnodytes*), diverged in Africa, with isolation of *T. pelzelni* and *T. rufolavatus* in Madagascar (80 to 90 MYBP). *T. ruficollis* reached the Eurasian continent and secondarily spread into the Austral-Asian region (well after *Poliocephalus*). *T. dominicus* (=*Limnodytes*) remained with South and Central America, eventually reaching the southern parts of North America. The other genus in the Podilymbini, *Podilymbus*, had ancestors that remained in South America, later diverging as *P. podiceps* and the flightless *P. gigas*. *P. podiceps* eventually invaded North America. The proposed zoogeographic pattern for the tribe Podilymbini is presented by dotted lines in Fig. 2.

The pattern for the tribe Podicipedini is more complex. Today, *P. cristatus* is not found in the New World, and there is no evidence that it ever existed there. *P. nigricollis* is found in North America, but occurs in South America only in small numbers and only in the northernmost part. Therefore, this model proposes an early divergence of the genus *Podiceps* into the small and large forms, with one representative of each, *P. cristatus* and *P. nigricollis* (or their ancestors), accompanying the African-Indian subcontinents as they separated from Gondwanaland. Later, both invaded Eurasia and secondarily, the Australian region while *P. nigricollis* followed the De Geer Route into North America, and later arrived in northern South America. Of the other Podicipedini, the primitive *"Podiceps" major* and the small forms remained in South America, where the latter diverged. Ancestral *P. grisegena-P. auritus-Aechmophorus* moved to North America. *Aechmophorus* split from this group in North America. Although fossil evidence is scant, the earliest record of *Aechmophorus* is of the Upper Pliocene (Murray, 1967). *P. grisegena* and *P. auritus* (or the ancestor) followed the De Geer Route into Eurasia. This pattern is represented by a solid line in Fig. 2.

The primitive genus, *Rollandia*, has remained in South America. This genus is represented by a dashed line in Fig. 2.

D. Phylogeny of the Amabiliidae

The family Amabiliidae comprises 19 species in three genera. Two of the genera, *Schistotaenia* and *Tatria*, occur only in grebes; the other, *Amabilia*, includes a single species found in flamingos. The affinity of *Amabilia lamelligera* to other amabiliids is questionable. Although *A. lamelligera* has postero-lateral processes on the proglottids and lacks vaginal apertures, other characteristics are not similar to those of *Schistotaenia* and *Tatria*. Wardle and McLeod (1952) concluded that the Amabiliidae served as a convenient grouping for these genera, but that no genetic relationships among the three should be implied. Ryzhikov and Tolkacheva (1975) recognized the dissimilarity and erected the sub-families Amabiliinae (containing *A. lamelligera*) and Schistotaeniinae (containing *Tatria* spp.

and *Schistotaenia* spp.). The genus *Amabilia* will not be considered further.

The genera *Schistotaenia* and *Tatria* contain 18 species. Eleven characters were used for cladistic analysis; four were two-state or binary characters, four characters each had three states, two had four states, and one, hook number, was considered to have six states (Table 2). Plesiomorphic (most generalized) states were coded as zeros. They were determined under the assumption that *Tatria* and *Schistotaenia* are related, and shared an ancestor that was intermediate in morphology. In addition, characters that are seen as general in most cyclophyllidean cestodes were considered plesiomorphic. Morphological characters of the 18 species (Table 3) were extracted from published species descriptions and taxonomic reviews; no specimens, other than those collected in this study, were directly examined. A non-quantitative approach (Hennig's argumentation scheme), as outlined in Brooks *et al.* (1984), was used to derive cladograms.

Derivations of the cladograms for both *Schistotaenia* and *Tatria* depend greatly on the validity of the characters used in the analysis. Misinterpretation of morphological features can result from several causes. Regular genital apertures may at first appear irregular if cirri have been ripped out of their pouches, as may happen for amabiliids that use a hypodermic impregnation method (see Chapt. 3). Also, poorly preserved specimens may lose rostellar hooks

Table 2. Character states used to derive cladograms for amabiliid tapeworms.

Character	State
1. Location of genital pores	irregular = 0
	regular = 1
2. Rostellar hook length	greater than 140 um = 2
	100 - 140 um = 1
	30 - 100 um = 0
	less than 30 um = -1
3. Number of rostellar hooks	more than 20 = 2
	20 = 1
	14 = 0
	12 = -1
	10 = -2
	8 = -3
4. Hook guard to blade ratio	greater than 1 = 0
	approximately 1 = 1
	less than 1 = 2
5. Number of testes	greater than 40 = 2
	20 - 40 = 1
	10 - 20 = 0
	less than 10 = -1
6. Rostellar spines	present = 0
	absent = 1
7. Shape of ovary	bilobed = 0
	elongate = 1
8. Length of cirrus	short (less than 1 mm) = 0
	long = 1
9. Length of the body	more than 10 mm = 1
	5 - 10 mm = 0
	less than 5 mm = -1
10. Body shape	club-shaped = 1
	parallel = 0
	cuneform = -1
11. Arrangement of testes	concentrated aporally = -1
	in two groups = 0
	in a row = 1

Table 3. Character states of species of amabiliid tapeworms.

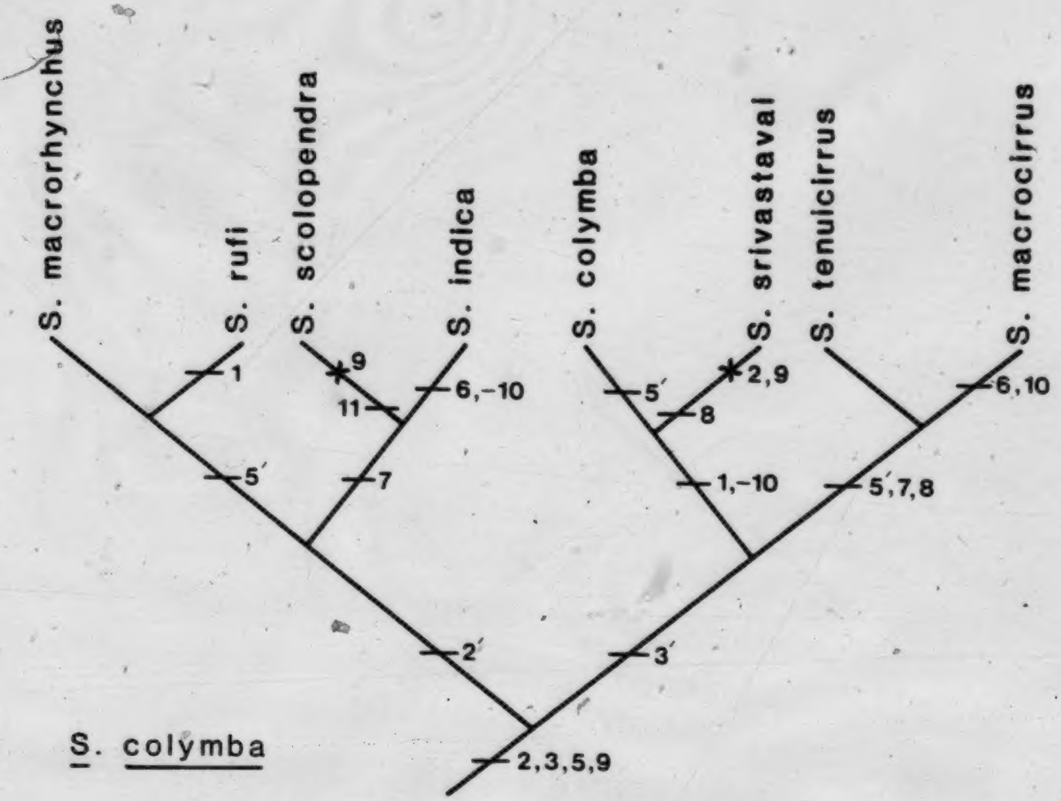
Species	Characters 1	2	3	4	5	6	7	8	9	10	11
Schistotaenia colymba	1	1	2	0	2	0	0	0	1	-1	0
Schistotaenia indica	0	2	1	0	1	1	1	0	1	-1	0
Schistotaenia macrocirrus	0	1	2	0	2	1	1	1	1	1	0
Schistotaenia macrorhynchus	0	2	1	0	2	0	0	0	1	0	0
Schistotaenia rufi	1	2	1	0	2	0	0	0	1	0	0
Schistotaenia scolopendra	0	2	1	0	1	0	1	0	0	0	1
Schistotaenia srivastavai	1	0	2	0	1	0	0	1	0	-1	0
Schistotaenia tenuicirrus	0	1	2	0	2	0	1	1	1	0	0
Tatria acanthorhyncha	1	-1	0	1	-1	0	0	0	0	-1	1
Tatria appendiculata	1	-1	-2	2	-1	1	0	0	-1	-1	1
Tatria biremis	1	0	-2	2	-1	0	0	0	-1	-1	1
Tatria decacantha	1	-1	-2	1	-1	0	0	0	0	-1	1
Tatria duodecacantha	1	-1	-1	2	-1	1	1	0	-1	-1	1
Tatria fuhrmanni	0	-1	0	1	0	0	1	0	0	-1	-1
Tatria inuii	1	-1	-2	1	-1	0	0	0	-1	-1	0
Tatria octacantha	1	-1	-3	1	-1	0	0	0	-1	-1	0
Tatria skrjabini	1	0	0	2	-1	0	0	0	-1	-1	1

and spines. Close examination of specimens, however, will reveal "scars" of both events, thus allowing a proper assessment. Ryzhikov and Tolkacheva (1977) show *Schistotaenia indica* as having a hook shape that is very different than that for other *Schistotaenia* species. Examination of the original description, however, showed that the hook shape of *S. indica* was typical. Ryzhikov and Tolkacheva chose hooks that were not drawn in the perpendicular plane as being typical of the species. Ovary shape, arrangement of the testes, body length and body shape can vary depending on the method of fixation and on the maturity of the worms examined. Therefore, some caution must be exercised when using these characters for cladistic analysis, particularly since in most cases actual specimens were not examined.

Ryzhikov and Tolkacheva (1977), in a review of the genus *Schistotaenia*, erected two sub-genera, *Schistotaenia* and *Paraschistotaenia*, on the basis of the position of the genital pores. *Paraschistotaenia* included three species, *S. colymba*, *S. rufi* and *S. srivastavai*, that have regularly alternating pores. The other five species, placed in the sub-genus *Schistotaenia*, have irregularly alternating pores. Using cladistic analysis, a single, most parsimonious, fully-resolved cladogram was derived (Fig. 3). This scheme does not agree with the proposed sub-generic designation of Ryzhikov and Tolkacheva. Rather than discriminating natural groups on the basis of genital pores, the cladogram with the

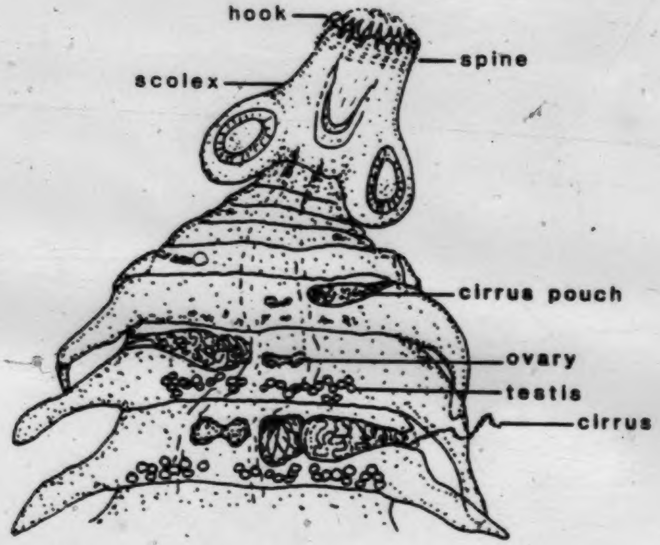
Figure 3. Cladogram depicting the phylogenetic relationships among species of the genus Schistotaenia.

Schistotaenia



× = Reversal

S. colymba



fewest reversals (3), and parallelisms (7), was based primarily on hook size and number. A cladogram based primarily on genital pore position had 5 reversals, and 6 parallelisms. The consistency index (the minimum number of steps required to derive a cladogram divided by the actual number of steps used, see Brooks *et al*., 1985) for the most parsimonious cladogram was 88%, versus 84% for the cladogram polarized by the placement of genital pores. The two cladograms resulted in the same pairings for six of eight species, but the placings of those pairs were different. The major differences involved the positions of *S. rufi* and *S. macrorhynchus*. In the most parsimonious cladogram, *S. macrorhynchus* was considered to be most closely related to *S. rufi*, whereas in the cladogram reflecting Ryzhikov and Tolkacheva's classification, *S. macrorhynchus* arises as an isolated species, close to the stem of the subgenus *Schistotaenia*.

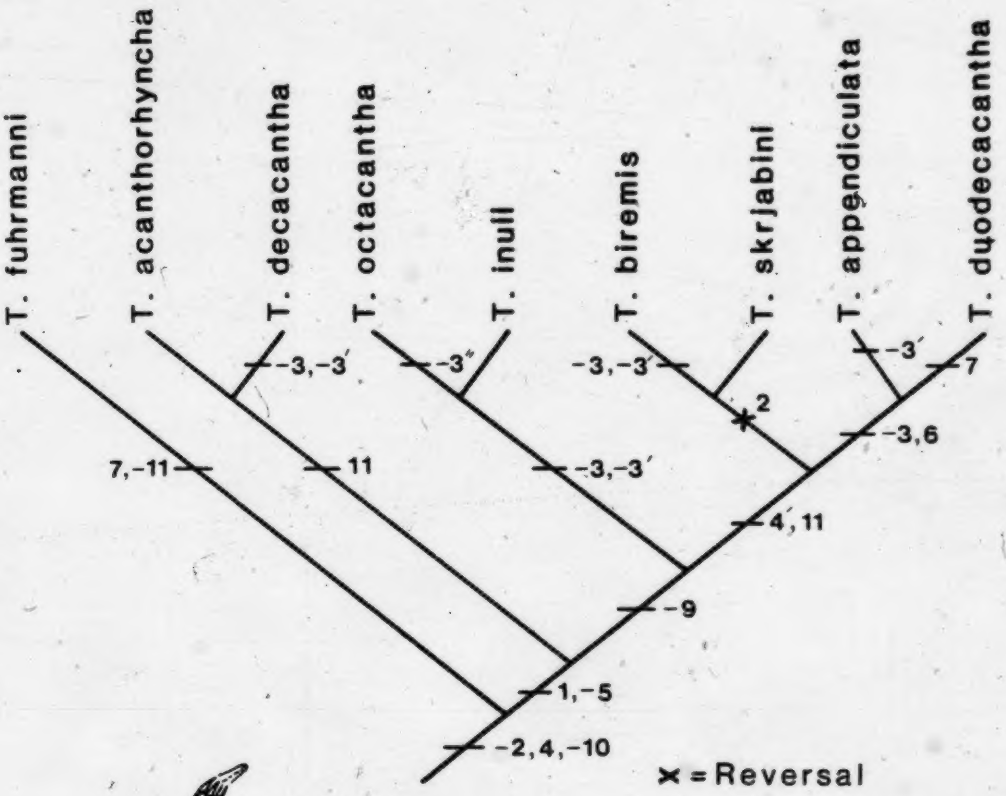
Both cladograms demonstrate a significant amount of parallelism of apomorphic characters (for instance, the reduced size of *S. srivastavai* and *S. scolopendra*; loss of rostellar spines by *S. macrocirrus* and *S. indica*; and elongated cirri in *S. srivastavai*, *S. tenuicirrus* and *S. macrocirrus*). Brooks (1977), however, pointed out that derived states can arise repeatedly and he concurred with the view of Bock (1963) that groups evolving in narrow adaptive zones, as parasites in hosts were presumed to be, exhibit higher degrees of homoplasy (*i.e.*, similarities not due to inheritance from a common ancestor; for example, convergence, analogy, mimicry and chance similarity) than those evolving in broader zones.

The genus *Tatria* includes ten species of cestodes that are smaller than *Schistotaenia*, have fewer rostellar hooks and fewer testes. Because the smaller worms are more subject to autolytic degeneration, including loss of rostellar hooks and breakdown of strobilas into individual proglottids, descriptions of species of *Tatria* are generally less complete and more ambiguous than those for *Schistotaenia*. One species, *Tatria azerbaijanica*, had to be deleted from the phylogenetic analysis because its description was unavailable and few of its characteristics have been cited in other studies.

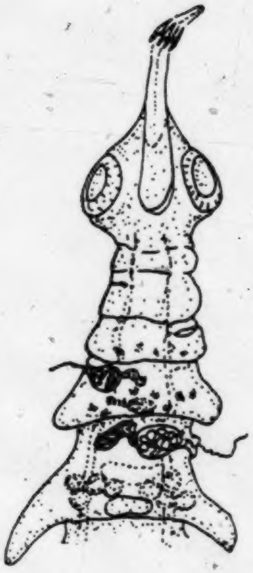
Rees (1973), impressed by the two markedly different types of hooks shown by species of *Tatria*, concluded that they defined two natural groups of species. The most parsimonious cladogram for species of *Tatria* preserved the species with elongated hook shape as a natural group, as suggested by Rees. However, this character (4' in Fig. 4) was not of primary importance as a discriminator. Body length, arrangement of genital pores, number of testes, and hook number were equally or more important. As for *Schistotaenia*, the cladogram demonstrated significant parallelism (8 occurrences), but only 1 reversal (consistency index, 91%). A cladogram based primarily on Rees's criterion had a total of 11 reversals and

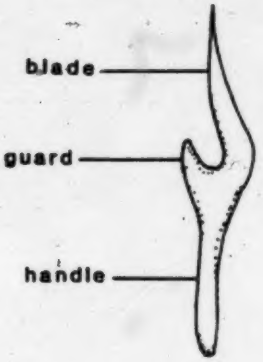
Figure 4. Cladogram depicting phylogenetic relationships among species of the genus Tatria.

Tatria



T. biremis





parallelisms (consistency index, 81%).

E. Comparison of Host and Parasite Genealogies

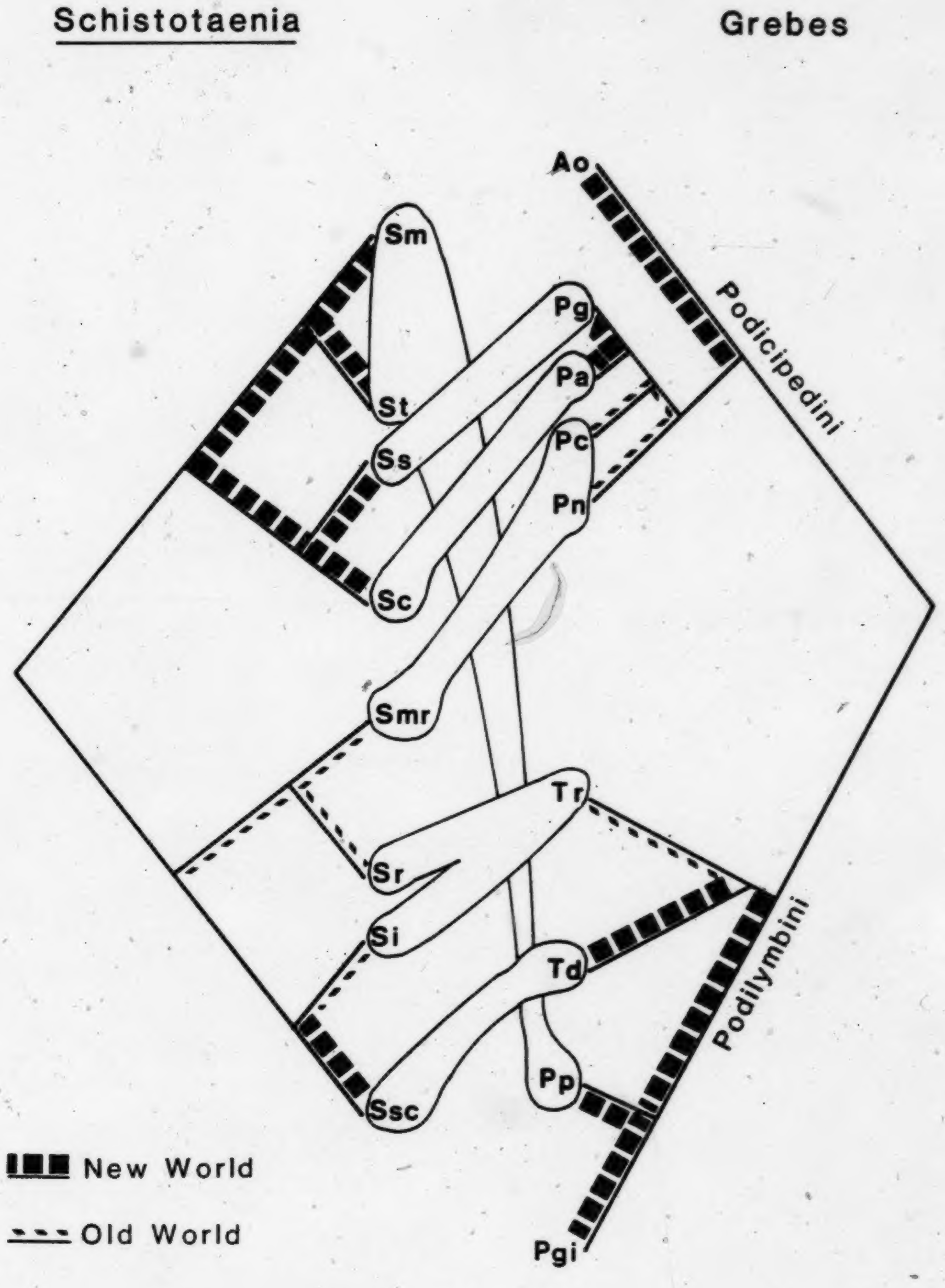
Matching the parasite cladograms to the host phylogenetic scheme requires resolution of the "normal" or main host for each parasite for which several hosts are known (Table 4). Where quantitative data are available, main hosts were those that were most frequently infected with the highest numbers of that particular parasite species. Using this criterion, *Podiceps grisegena* was considered the main host of *Tatria decacantha*, and *P. nigricollis* the main host for *T. biremis* (based on data in Korpaczewska and Sulgostowska, 1974; and in Chapt. 3). The host of *Tatria fuhrmanni*, was reported simply as a "grebe" from East Africa (Solomon, 1932); because *Podiceps cristatus*, *P. nigricollis* and *Tachybaptus ruficollis* all occur in this region, the main host is unknown. For several cestodes, the main host is uncertain (Table 4); however, zoogeographic patterns make it possible to suggest a species of grebe as a main host. These will be examined later.

Comparison of *Schistotaenia* and grebe genealogies demonstrated both zoogeographic and cospeciation patterns (Fig. 5). The major separation in the *Schistotaenia* cladogram is between species found in New World hosts *Podiceps grisegena*, *P. auritus*, and *Podilymbus podiceps*, versus those from Old World hosts - *Tachybaptus ruficollis* and *Podiceps nigricollis*. The only exception to this

Table 4. Main hosts and locations of amabiliid tapeworms.

Parasites	Main host(s)	Location
Schistotaenia colymba	*Podiceps auritus*, *P. nigricollis*	North America
Schistotaenia indica	*Tachybaptus ruficollis*	India
Schistotaenia macrocirrus	*Podilymbus podiceps*	United States
Schistotaenia macrorhynchus	*Podiceps cristatus*, *P. nigricollis*, *T. ruficollis*	Eurasia, Africa
Schistotaenia scolopendra	*Tachybaptus dominicus*	Cuba, Brazil
Schistotaenia rufi	*Tachybaptus ruficollis*	Poland
Schistotaenia srivastavai	*Podiceps grisegena*	North America
Schistotaenia tenuicirrus	*Podilymbus podiceps*	United States
Tatria acanthorhyncha	*Tachybaptus ruficollis*, *Podiceps* spp.	Eurasia, India, Japan
Tatria appendiculata	*Tachybaptus dominicus*	Cuba
Tatria biremis	*Podiceps nigricollis*	North America, Europe
Tatria decacantha	*Podiceps grisegena*	North America, Europe
Tatria duodecacantha	*Podilymbus podiceps*	United States
Tatria fuhrmanni	"*Podiceps*" ?	Africa
Tatria inuii	*Tachybaptus ruficollis*	Poland
Tatria octacantha	*Tachybaptus ruficollis*	Great Britain
Tatria skrjabini	*Tachybaptus ruficollis*	Soviet Union

Figure 5. A comparison of the genealogies of the parasites, *Schistotaenia* spp., and their grebe hosts. Lines connect parasites with their main hosts.


Schistotaenia
Grebes
Ao
Sm
Pg
Podicipedini
Pa
St
Pc
Ss
Pn
Sc
Smr
Tr
Sr
Si
Podilymbini
Td
Pp
Ssc
Pgi
▮▮▮ New World
- - - Old World

dichotomy involves *S. scolopendra*, which occurs in a New World host, *T.* (=*Limnodytes*) *dominicus*. Superimposed on this pattern is one of co-speciation. Four tapeworms, *S. srivastavai*, *S. colymba*, *S. indica* and *S. scolopendra*, show phylogenetic matching with their hosts. The three possible examples of host capture, *S. rufi* in *T. ruficollis*, *S. macrorhynchus* in *P. nigricollis* (also reported from *T. ruficollis*), and *S. macrocirrus* and *S. tenuicirrus* in *Podilymbus podiceps*, are congruent with the zoogeographic pattern. This suggests the hypothesis that the host capture events, at least for *S. tenuicirrus*, *S. macrocirrus* and *S. rufi*, occurred early during the evolution of grebes. The comparison also shows that the "*Tachybaptus*" group of tapeworms had divided into two stocks during the breakup of Gondwanaland, suggesting a very old association between *Schistotaenia* and grebes.

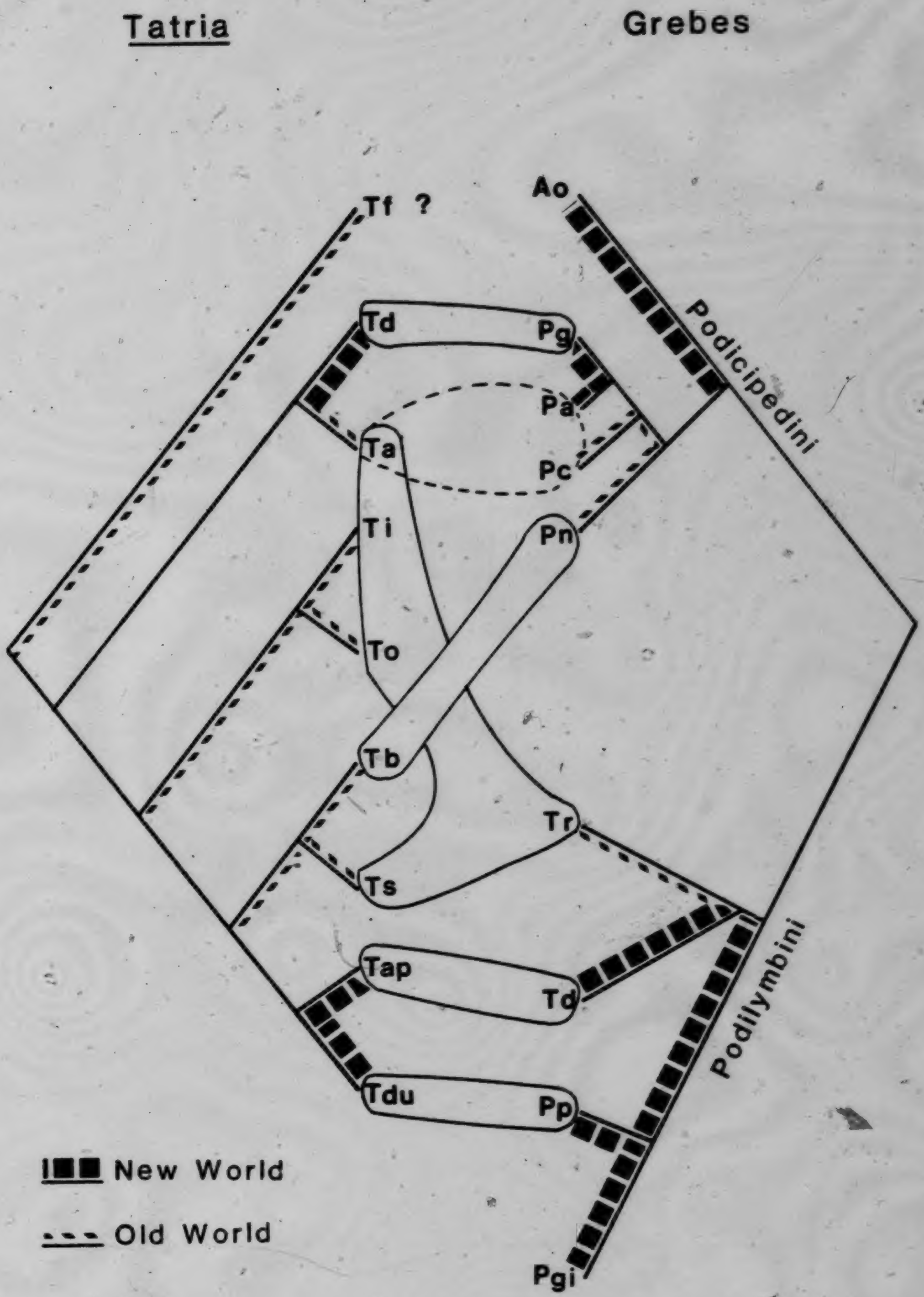
Ryzhikov and Tolkacheva's scheme supports most of these conclusions. Most of the *Paraschistotaenia* species occur in the Podicipedini, while most of the *Schistotaenia* species occur in the Podilymbini. Host capture events, including *Tachybaptus* by *S. rufi*, and *Podiceps* by *S. macrorhynchus*, both demonstrate the zoogeographic pattern. Therefore, both schemes for the phylogenetic relations of *Schistotaenia* reflect a mixture of co-speciation and zoogeography; however, they differ in emphasis. The preferred cladogram emphasizes zoogeography, Ryzhikov and Tolkacheva's scheme, co-speciation. Both advocate an old, long-standing association between parasites and hosts.

The *Tatria* cladogram, when compared to the phylogenetic scheme for grebes, also manifests a combined zoogeographic and co-speciation pattern (Fig. 6). Five species, *T. duodecacantha*, *T. appendiculata*, *T. octacantha*, *T. inuii* and *T. decacantha*, illustrate co-speciation with their hosts. Both major branches of the cladogram show New World -Old World splits. The *T. duodecacantha- T. appendiculata* branch and the *T. decacantha* branch are New World sections of the cladogram, while the remaining branches represent the Old World sections.

Two cases of colonization (host capture) are apparent. Based on the tapeworm cladogram, *T. biremis* appears to have evolved from an Old World ancestor that infected a grebe in the *Tachybaptus* lineage. The primary host, however, is the Old World *Podiceps nigricollis*. Korpaczewska and Sulgostowska (1974), recognized two subspecies of *T. biremis*, *T. b. minor*, specialized in *P. nigricollis*, and *T. b. major* in *P. grisegena*, *P. nigricollis*, *P. cristatus*, and *T. ruficollis*. Specialization of one of the races for *P. nigricollis* supports an interpretation of *P. nigricollis* as the main host for *T. biremis*. This pattern of host capture, in relation to the proposed zoogeographic supposition, points to a long relationship.

The second possible case of a host capture involved *T. acanthorhyncha*. The species has frequently been reported in *P. nigricollis*, *P. grisegena*, *P. cristatus*, and *T.*

Figure 6. A comparison of the genealogies of the parasites, _Tatria_ spp., and their grebe hosts. Lines connect parasites with their main hosts, dashed line indicates other potential main hosts, see text for details.


Tatria
Grebes
Tf ?
Ao
Td
Pg
Podicipedini
Pa
Ta
Pc
Ti
Pn
To
Tb
Tr
Ts
Tap
Td
Podilymbini
Tdu
Pp
Pgi
New World
Old World

ruficollis. Ryzhikov and Tolkacheva (1975) considered *P. cristatus* as the main host for this parasite; Okorokov (1956) reported *P. cristatus* and *P. nigricollis*, but Korpaczewska and Sulgostowska (1974) reported higher prevalence and intensity infections in *T. ruficollis* than in *P. grisegena* or *P. nigricollis* in Poland. If *T. ruficollis* is the main host, then the evolutionary pattern is one of host capture; if *P. cristatus* or *P. nigricollis* is the main host, then the pattern is one of co-speciation. Either pattern is congruent with a zoogeographic pattern since all possible main hosts are Old World. A scheme based on Rees' criterion, which considered hook shape to be a polarizing feature, was less closely matched with host phylogeny, but still illustrated the zoogeographic pattern.

The comparison of genealogies between *Tatria* and grebes, like that for *Schistotaenia*, is impeded by the lack of characters available for use in the analysis, and by the large number of grebe species that have not been examined for parasites. However, the comparisons for both genera of amabiliids with grebes indicated that the zoogeographic divergence between Old World and New World hosts, which probably occurred in the mid to late Cretaceous, was a decidedly important coevolutionary event.

Within the Podicipedini, long term contacts were implicated between *P. grisegena* and *S. srivastavai* and *T. decacantha*, and between *P. nigricollis* and *T. biremis*, *T. acanthorhyncha* (and possibly *S. macrorhynchus*). Within the

Podilymbini, long term contacts were noted between the following: *Podilymbus podiceps* and *S. macrocirrus*, *S. tenuicirrus* and *T. duodecacantha*; *T. ruficollis* and *S. indica* (and possibly *S. rufi* and *S. macrorhynchus*), *T. inuii*, *T. octacantha*, *T. skrjabini* (and possibly *T. acanthorhyncha*); and *T. dominicus* and *S. scolopendra* and *S. appendiculata*. Extensive co-speciation between hosts and tapeworms is evident, and cases of host capture are coincident with the zoogeographic pattern. All evidence points to a long host-parasite association.

F. Implications for Intestinal Helminth Community Structure

In *P. grisegena* and *P. nigricollis*, the congeneric pair of *T. decacantha* and *T. biremis* had different intensities of infection, and utilized different microhabitats (Chapt. 3). *T. biremis* has elongated rostellar hooks and a smaller body than *T. decacantha*, and occurred in the proximal intestine. *T. decacantha* has smaller hooks, and occurred in the mid intestine. These species conformed to a general pattern in which tapeworms with long, well-developed rostellar hooks occurred more anteriad in the intestine than species with reduced hooks or those lacking hooks altogether (see Chapt. 3). *T. acanthorhyncha* and *T. decacantha* are sister species; both are relatively large species and both have reduced, squat-shaped hooks. They are probably ecological equivalents and would be expected to occupy the same part of the intestine. The coexistence of either with *T. biremis* is probable, but they would not be expected to co-occur.

A similar group of three species (possibly four, counting *T. acanthorhyncha*) occurs in *Tachybaptus ruficollis*. *Tatria skrjabini* has elongate hooks, while *T. inuji* and *T. octacantha* resemble *T. acanthorhyncha* in having small, squat hooks. Based on the hook length - position correlation, I predict that *T. skrjabini* would be located in the proximal intestine of *T. ruficollis*, but *T. inuii* and *T. octacantha* would be found more posteriad. As in the example above, *T. inuii* and *T. octacantha* and *T. acanthorhyncha* are probably equivalents, and therefore, would not frequently co-occur. These species may be geographically isolated; *T. inuii* was reported from eastern Europe (Poland), while *T. octacantha* has been reported only from England. *T. acanthorhyncha* is distributed throughout Eurasia (see Rees, 1973).

The two species of *Schistotaenia* for which precise locations are known, *S. srivastavai* and *S. colymba*, had similar shaped hooks of about the same length, and occurred in the same location in the proximal intestines of their hosts. Hook lengths for other species (*e.g.*, *S. scolopendra*, *S. macrorhynchus*) were longer. Perhaps they are found more anterior in the intestine. However, all species on the Old World side of the *Schistotaenia* cladogram had long hooks, which suggests that hook length may be a function of the geographical/evolutionary history of these species, as well as being an adaptation for their location within the intestine.

Brooks (1979) felt that coevolution between hosts and parasites encompassed two separate phenomena: co-accommodation and co-speciation. Co-accomodation incorporated mutual adaptations between hosts and parasites expressed in differences in pathogenicity, host specificity and synchrony of life cycle stages to ensure transmission. The distinction between specialist and generalist parasites resided in differences in co-accommodation. Co-speciation involved the cladogenesis of an ancestral parasite in response to host cladogenesis.

For *Schistotaenia*, parasites generally demonstrated narrow co-accommodation. *S. srivastavai*, *S. scolopendra*, and *S. indica* are known to infect predominently a single host species. *S. colymba*, described from *P. auritus*, is common in *P. nigricollis* from North America (52%, see Chapt. 2), and may be regarded as having wider co-accommodation. Based on those species known, it appears that *Schistotaenia* species are very narrowly co-accommodated with respect to their position within the intestine (Chapt. 3). Most *Tatria* species, however, have been reported from several hosts and exist in a wider area within their hosts, therefore, they may be considered to have broader co-accommodation.

No species of *Schistotaenia* were found in *Aechmophorus occidentalis*. Although both *Tatria biremis* and *T. decacantha* were found in that host, both occurred at low prevalence and in low numbers. *A. occidentalis*, specialized for feeding on fish, probably does not consume many odonate nymphs which serve as intermediate hosts for amabiliids. *P. cristatus*, also known to feed predominently on fish, is also not infected by *Schistotaenia*, but does have *Tatria* infections. This suggests that host food habits make a significant contribution to the patterns of host - parasite association.

Fjeldsa (1983) studied ecological segregation and resource exploitation of grebes in northern Europe, South America and Australia. In every case in which two similar grebe species were sympatric, one or both showed indications of divergent bill morphology, leading to reduced interspecific food overlap. The data suggested character displacement indicative of coevolution in grebe faunas. Differences in feeding are likely to favor differences in transmission of various parasites. This would sustain and intensify trends toward narrow co-accommodation.

Therefore, all data advocate a long and recurrent association between the amabiliid core species and their grebe hosts. Patterns of differential host infection and selective site segregation, in conjunction with coevolution, point to an old, well-adjusted helminth community. Analysis of the communities of helminths in other grebes, and cladistic analysis of other core helminths, would provide further evidence for the evaluation of this hypothesis.

G. Bibliography

Baer, J.G. 1940. Some avian tapeworms from Antigua. Parasitology 32:174-197.

Bock, W.J. 1963. Evolution and phylogeny in morphologically uniform groups. Amer. Natur. 97:265-285.

Brooks, D.R. 1977. Evolutionary history of some plagiorchioid trematodes in anurans. Syst. Zool. 26:277-289.

Brooks, D.R. 1979. Testing the context and extent of host-parasite coevolution. Syst. Zool. 28:299-307.

Brooks, D.R. 1980. Allopatric speciation and non-interactive community structure. Syst. Zool. 29:192-203.

Brooks, D.R., J.N. Caira, T.R. Platt, and M.H. Pritchard. 1984. Principles and Methods of Phylogenetic Systematics: A Cladistics Workbook. Spec. Publ. No. 12 Mus. Nat. Hist., Univ. Kansas. 92 pp.

Brown, J.H., and A.C. Gibson. 1983. Biogeography. C.V. Mosby Co., St. Louis. 643 pp.

Chandler, A.C. 1948. New species of the genus *Schistotaenia*, with a key to the known species. Trans. Amer. Micr. Soc. 77:169-176.

Cracraft, J. 1973. Continental drift, paleoclimatology, and the evolution and biogeography of birds. J. Zool. London. 169:445-546.

Cracraft, J. 1982. Phylogenetic relationships and the monophyly of loons, grebes, and hesperornithiform birds, with comments on the early history of birds. Syst. Zool. 31:35-56.

Cramp, S., and K.E.L. Simmons. 1977. Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic. Vol. 1. Ostrich to Ducks. Oxford Univ. Press, Oxford. 722 pp.

Fager, E.W. 1957. Determination and analysis of recurrent groups. Ecology 38:586-595.

Fager, E.W., and J.A. McGowan. 1963. Zooplankton species groups in the North Pacific. Science 140:453-460.

Feduccia, A. 1980. The Age of Birds. Harvard Univ. Press, Cambridge, Mass. 196 pp.

Fjeldsa, J. 1983. Ecological character displacement and character release in grebes, Podicipedidae. Ibis 125:463-481.

Hanski, I. 1982. Dynamics of regional distribution: The core and satellite species hypothesis. Oikos 38:210-221.

Holmes, J.C. 1971. Habitat segregation in sanguinicolid blood flukes (Digenea) of scorpaenid rockfishes (Perciformes) on the Pacific coast of North America. J. Fish. Res. Board Can. 28:903-909.

Holmes, J.C. 1973. Site selection by parasitic helminths: Interspecific interactions, site segregation, and their importance to the development of helminth communities. Can. J. Zool. 51:333-347.

Holmes, J.C. 1983. Evolutionary relationships between parasitic helminths and their hosts. pp. 161-185 In D.J. Futuyma and M. Slatkin (eds.), Coevolution. Sinauer Assoc. Inc., Sunderland, Mass. 555 pp.

Holmes, J.C., and P.W. Price. 1980. Parasite communities: The roles of phylogeny and ecology. Syst. Zool. 29:203-213.

Holmes, J.C., and P.W. Price. 1985. Communities of Parasites. In D.J. Anderson and J. Kikkawa (eds.), Community Ecology: Pattern and Process. Blackwell Sci. Co., Oxford.

Jogis, V. 1978. On some morphobiological peculiarities of *Dioecocestus asper* (Cestoda: Acoelidae) and on the origin of dioecy. (In Russian.). Proc. Eston. SSR. Acad. Sci. 27:118-124.

Johri, G.N. 1959. Descriptions of two amabiliid cestodes from the little grebe, *Podiceps ruficollis*, with remarks on the family Amabiliidae Braun, 1900. Parasitology 49:454-461.

Korpaczewska, W. 1960. Some reflections on *Hymenolepis furcifera* Krabbe 1869 and related species. Acta Parasit. Polon. 8:461-470.

Korpaczewska, W., and T. Sulgostowska. 1974. Revision of the genus *Tatria* Kow., 1904 (Cestoda: Amabiliidae), including a description of *Tatria inuii* sp. n. Acta Parasit. Polon. 22:67-91.

Martin, D.R. 1969. Lecithodendriid trematodes from the bat, *Peropteryx kappleri* in Columbia, including discussions of allometric growth and significance of ecological isolation. Proc. Helm. Soc. Wash. 36:250-260.

Mitter, C., and D.R. Brooks. 1983. Phylogenetic aspects of coevolution. pp. 65-98. In D.J. Futuyma and M. Slatkin (eds.), Coevolution. Sinauer Assoc. Inc., Sunderland, Mass. pp. 555.

Murray, B.G.,Jr. 1967. Grebes from the late Pliocene of North America. Condor 69:277-288.

Okorokov, V.I. 1956. A new species of cestode *Tatria mathevossianae* (Family Amabiliidae) from *Podiceps ruficollis* (Pallas). (In Russian.). Zool. Zhur. 35:1299-1302.

Olsen, O.W. 1939. *Tatria duodecacantha*, a new species of cestode (Amabiliidae Braun, 1900) from the pied-billed grebe (*Podilymbus podiceps podiceps* (Linn.)). J. Parasit. 25:495-499.

Palmer, R.S. 1962. Handbook of North American Birds. Vol. 1. Loons through Flamingos. Yale University Press, New Haven, Conn. 567 pp.

Price, P.W. 1980. Evolutionary Biology of Parasites. Princeton Univ. Press, Princeton, N.J. 160 pp.

Price, P.W. 1984. Communities of specialists: Vacant niches in ecological and evolutionary time. pp. 510-523. In D.R. Strong, Jr., D. Simberloff, L.G. Abele, and A.B. Thistle (eds.), Ecological Communities: Conceptual Issues and the Evidence. Princeton Univ. Press, Princeton, N.J. 613 pp.

Rausch, R.W. 1970. Studies on the helminth fauna of Alaska XLV. *Schistotaenia srivastavai* n. sp. (Cestoda: Amabiliidae) from the red-necked grebe, *Podiceps grisegena* (Boddaert). H.D. Srivastavai Commem. Vol. pp. 109-115.

Rees, G. 1973. Cysticercoids of three species of *Tatria* (Cyclophyllidea: Amabiliidae) including *T. octacantha* sp. nov. from the haemocoel of the damsel-fly nymphs *Pyrrhosoma nymphula*, Sulz and *Enallagma cyathigerum*, Charp. Parasitology 66:423-446.

Rich, P.V. 1983. Commentary to Chapter 9. pp. 345-353 In A.H. Brush and G.A. Clark, Jr. (eds.), Perspectives in Ornithology. Cambridge Univ. Press, Cambridge, Mass. 560 pp.

Rohde, K. 1979. A critical evaluation of intrinsic factors responsible for niche restriction in parasites. Amer. Natur. 114:648-671.

Roughgarden, J. 1983. The theory of coevolution. pp. 33-64 In D.J. Futuyma and M. Slatkin (eds.), Coevolution. Sinauer Assoc. Inc., Sunderland, Mass. 555 pp.

Rysavy, B., and J.K. Macko. 1971. Bird cestodes of Cuba. I. Cestodes of birds of the orders Podicipediformes, Pelicaniformes and Ciconiiformes. An. Inst. Biol. Univ. Nal. Auton. Mexico 42:1-28.

Ryzhikov, K.M., and L.M. Tolkacheva. 1975. Taxonomic review of the family Amabiliidae (Cestoda, Cyclophyllida). (In Russian.) Zool. Zhur. 54:498-502.

Ryzhikov, K.M., and L.M. Tolkacheva. 1977. Morpho-taxonomic characters representative of the genus *Schistotaenia* Cohn, 1900 (Amabiliidae, Acoleata). (In Russian.) Trud. Gelmin. Lab. 27:205-211.

Sanders, S.W.H. 1967. The osteology and myology of the pectoral appendage of grebes. Ph. D. thesis. Univ. of Michigan, Ann Arbor, Mich. 281 pp.

Schell, S.C. 1955. *Schistotaenia colymba* n. sp. from the horned grebe (*Colymbus auritus* L.). Trans. Am. Micro. Soc. 74:347-350.

Schultz, R.L. 1940. Some observations on the amabiliid cestode, *Tatria duodecacantha* Olsen, 1939. J. Parasit. 26:101-104.

Simmons, K.E.L. 1954. The advertising behavior of the great crested grebe. Bird Study 1:53-56.

Simmons, K.E.L. 1968. Winter flocking and behaviour of little and great crested grebes. Brit. Birds 61:556-558.

Simmons, K.E.L. 1974. Adaptations in the reproductive biology of the great crested grebe. Brit. Birds 67:413-437.

Smyth, J.D. 1966. The Physiology of Cestodes. Oliver and Boyd, Edinburgh. 279 pp.

Sogandares-Bernal, F. 1959. Digenetic trematodes of marine fishes from the Gulf of Panama and Bimini, British West Indies. Tulane Stud. Zool. 7:69-117.

Solomon, S.G. 1932. On a collection of parasitic worms from East Africa. J. Helminthol. 10:209-230.

Spasskaija, L.P. 1966. Cestodes of Birds of the USSR. (In Russian.) Akad. Sci. USSR, Moscow. 698 pp.

Stettenheim, P. 1974. The bristles of birds. Living Bird 12:201-234.

Storer, R.W. 1961. Observations of pellet-casting by horned and pied-billed grebes. Auk 78:90-92.

Storer, R.W. 1963a. Courtship and mating behavior and the phylogeny of grebes. Proc. XIII Intern. Ornithol. Congr. pp. 562-569.

Storer, R.W. 1963b. Observations on the great grebe. Condor 65:279-288.

Storer, R.W. 1967a. The patterns of downy grebes. Condor 69:469-478.

Storer, R.W. 1967b. Observations on Rolland's grebe. El Hornero 10:339-349.

Storer, R.W. 1971. The behaviour of the New Zealand dabchick. Notornis 18:175-186.

Storer, R.W. 1976. The Pleistocene pied-billed grebes (Aves: Podicipedidae). S.L. Olson, (ed.), Smithsonian Contributions to Paleobiology 27:147-153.

Sulgostowska, T., and W. Korpaczewska. 1969. *Schistotaenia rufi* sp. n. (Cestoda: Amabiliidae). Acta Parasit. Polon. 17:131-137.

Voous, K.H., and H.A.W. Payne. 1965. The grebes of Madagascar. Ardea 53:9-31.

Wardle, R.A., and J.A. McLeod. 1952. The Zoology of Tapeworms. Hafner Pub. Co., New York. 780 pp.

Wetmore, A., and K.C. Parkes. 1954. Notes on the generic affiliations of the great grebe of South America. J. Wash. Acad. Sci. 44:126-127.